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MORPHOLOGY OF THE POLLINIA AND POLLINARIA OF ORCHIDS FROM SOUTHEAST MEXICO

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ABSTRACT: This is a report of a morphological study of the pollinaria and pollinia of 91 species of orchids native to the region of Soconusco in southeast Mexico. A Scanning Electron Microscope (SEM) was used to obtain details of forms and patterns. The 91 species are divided according to taxonomic groups into 4 sections for ease of management. The flowering dates for each species are presented, and the pollinaria and pollinia are characterized and compared using the following parameters: number of pollinia per pollinarium; size and shape of the individual pollinia; details of the caudicles (if present); size of stipe (if present); internal texture of the pollinia; size and form of the tetrads; and finally, the form, superficial exine layer and internal exine layer, of the surface tetrads. The data and images will be useful for taxonomic studies, for the identification of pollinaria carried by pollinating insects and birds, and for continuing research into the mechanisms of orchid pollination.

Key words: epiphytic orchids, terrestrial orchids, orchid pollination, Soconusco

INTRODUCTION

The sexual reproduction of orchids is a highly complex affair involving many different types of pollinators (usually insects and birds) and a specialized structure (the pollinarium) which sticks to the body of the pollinator and should then, theoretically, be transported to the stigma of another orchid flower. However, orchids are well known for their low levels of seed set. In reality, many flowers never receive that vital visit, and even if they do, the pollinarium may never reach its destination.

The great majority of orchids present their pollen in discrete masses termed pollinia, which, in turn, are connected by additional structures to the anther. The additional structure may be a caudicle or stipe, or in some cases, simply a sticky substance which connects the pollinia to the viscidium and then unites them to the anther. Within each orchid flower, usually 2 or 4 pollinia, but sometimes up to 8 or 12 pollinia, and their additional structures combine to form a single structure, the pollinarium (Cribb 1999).

A caudicle is usually found in combination with hard and/or compact pollinia. The structure of the caudicle may vary; Dressler (1981) divided them into three major groups: bony, granular and hyaline. Bony caudicles are rarely found associated with hard pollinia (but see *Neowilliamsia*); granular caudicles are mainly composed of pollen grains (e.g., *Calanthe* and *Epidendrum*); and the hyaline caudicles are translucent and elastic with no cells and are composed mainly of elastoviscin, as occurs in the majority of the Vandoideae.

Many vandoid orchids, as well as some others, present a band of non-sticky tissue called the stipe that is derived from rostellum tissue instead of tissue from the anther (Cribb 1999).

The viscidium is a structure composed of part cells and part gum. In the majority of species of *Epidendrum,* the cells of the viscidium break up completely during anthesis and are converted into a gummy substance whose chemical composition resembles that of a glucoprotein and is secreted to serve as the only source of glue (Yeung 1987b, Schlee & Ebel 1983).

The number of pollinia is determined by the structure of the anther and number of loculi present. Many orchids have four pollinia per flower, representing four anther cells. In Epidendreae and Arethuseae, the ancestral number is eight; these can have a globular or clavate shape or can be bilaterally flattened. In the subtribes Laeliinae and Pleurothallidinae, of the tribe Epidendreae, a reduction can be observed from eight to six to four and finally to two pollinia. Some members of the Epidendroideae lack septation in the meristematic region of the anther, giving rise

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to the development of only two pollinia (Freudenstein & Rasmussen 1996). The number of pollinia per anther (generally 2, 4, 6 or 8) is constant at species level and often at genus, subtribe and tribe levels also. The number of compact pollinia per pollinarium is easy to define; but in the case of mealy pollinia, it can be difficult to distinguish between two profoundly lobed pollinia and four interconnected pollinia (Dressler 1993).

The unity of pollen grains is maintained by elastoviscin, a substance derived either from the tapetum of the anther or from the pollen exine. All tetrads have an exine layer on the external wall. Fitzgerald et al. (1994) studied the evolution of the way in which the pollen grains can be packed together to form pollinia with different textures, from the less evolved floury texture, to hard compact types, and all intermediate stages from floury to bony. The tetrads of floury pollinia separate easily, as seen in *Pterostylis* (Fitzgerald et al. 1994). In the majority of the Spiranthoideae and Orchidoideae, as well as the primitive Epidendroideae, the pollinia are denominated soft, whereas in the majority of the advanced Epidendroideae the pollinia are hard enough to be termed bony. Pacini and Hesse (2002) affirmed that the most common type of pollen dispersal unit (PDU) among the orchid family is the soft pollinium, type C, and described a group of pollinia, each consisting of a mass of tetrads joined by shared walls, as found in the Spiranthoideae, Orchidoideae and Epidendroideae.

The wall of an individual, mature, pollen grain is another distinguishing feature, and the formation and structure of these walls have been subject to intensive study. In the Orchidaceae, there are two main variations in the structure of the walls: 1) exine is present on the walls of all pollen grains, but only those found on the edge of the pollinia have a thick and ornamented exine layer, e.g., *Epidendrum scutella* and *Catasetum discolor,* or 2) the exine layer is present and well defined only in the external walls of the tetrads, e.g., *Epidendrum ibaguense, Catasetum discolor, Oeceoclades saundersiana* and *Loroglossum hircinum* (Yeung 1987a, Pacini & Hesse 2002).

In the largest tetrads or pollen units, the individual grains can be united by a continuous membrane of exine (calymmate) or covered by an individual exine layer (acalymmate), which is generally reduced on the internal face, making it possible to distinguish the arrangement of the tetrad (Faegri & Iversen 1989, Konta & Tsuji 1982).

Although the scanning electron microscope (SEM) is not the traditional method for the study of pollen morphology, it offers particularly valuable details of forms and patterns that cannot be visualized by either the transmission electron microscope (TEM) or the optical microscope (OM) (Moore et al. 1991). From the literature, examples of the application of SEM to the study of orchid pollen and pollinia can be seen in the morphological study of the pollen of Chloraeinae (Orchidaceae: Diurideae) and related tribes (Ackerman & Williams 1981), and the revision of the morphology of the subtribe Pleurothallidinae Lindl., using both SEM and TEM (Stenzel 2000).

The region of Soconusco is situated in the extreme southeast of Mexico, in the state of Chiapas (latitude 16° N; longitude 92° W), on the border with Guatemala. It is a tropical, humid region, with seasonal rainfall, rich in biodiversity and with diverse natural and agricultural ecosystems. The region has undergone environmental degradation in recent years due to overpopulation and aggressive and inadequate land management and now suffers the consequences of severe erosion, flooding and landslides, which in 1998 and again in 2005 reached crisis point. The project "Ecology and Sustainable Cultivation of Native Orchids in Soconusco" is dedicated to the search for mechanisms for the conservation of native orchids, albeit within restored habitats or within agroecosystems. Research work covers various aspects of orchid ecology, including pollination, which can be a bottleneck in deteriorated ecosystems where pollinators may be scarce or absent and orchid populations are small, few, and widely scattered. The present study of the morphology of the pollinia of Soconuscan orchids was motivated by the need for a detailed data base to enable us to identify the pollinaria, pollinia, stipes and caudicles carried on the bodies of pollinating insects and birds captured during observations and controlled experiments on pollination.

Materials and Methods

The biological material, consisting of fresh flowers from 91 species of orchids, divided into 4 taxonomic sections, is shown in Table 1A, including the date and place of collection and the accession number. The species studied are listed alphabetically in Table 1B. The specimens were collected from 1) the field (fragments of tropical rain forest and traditional coffee plantations); 2) native orchids collected from various localities in Soconusco and maintained in the Regional Botanical Garden "El Soconusco" (municipality of Tuzantán, Chiapas; altitude 80m; 15°07′03″N; 92°24′53″W) and its annex, Orchidarium "Santo Domingo" (municipality of Unión Juárez, Chiapas; altitude 900 m; 15°01′48″N; 92°06′21″W); and 3) from rustic and sustainable orchid cultures in rural communities in the Soconusco region, which

TABLE 1. List of orchid species studied, with collection data.

Section 1: 1

Species	Flowering date	Collection site	Accession number (voucher)
Subfamily Orchidoideae			
Tribe Cranichideae			
Subtribe Spiranthinae			
Aulosepalum hemichreum (Lindl.) Garay.	28 January 2004 and 23 January 2005	SD	54
Sarcoglottis sp. × 2	19 March 2005	JB	332, 331
Sarcoglottis sceptrodes (Rchb.f.) Schltr.	6 February 2004	JB	339
Subfamily Epidendroideae			
Tribe Sobralieae			
Elleanthus cynarocephalus (Rchb.f.) Rchb.f.	28 August 2005	SD	397
Sobralia macrantha Lindl.	18 May 2005	LP	220
Subtribe Bletiinae			
Coelia macrostachya Lindl.	20 September 2005	SD	436
Tribe Epidendreae			
Subtribe Ponerinae			
Isochilus carnosiflorus Lindl.	4 May 2004 and 2 May 2005	SD	111
Isochilus aff. *latibracteatus* A. Rich & Galeotti	2 May 2005	SD	113
Isochilus aff. *linearis* (Jacq) R. Br.	Data lost		501
Isochilus aff. *major* Cham. & Schltr.	25 May 2005	SD	261
Isochilus sp.	6 August 2004	SD	282
Nemaconia striata (Lindl.) van der Berg.	26 January 2005	SD	208

Section 1: 2

Species	Flowering date	Collection site	Voucher
Tribe Epidendreae			
Subtribe Laeliinae			
Barkeria obovata (C. Presl.) Christenson	7 January 2004 and 3 January 2005	JB	378
Barkeria skinneri (Bateman ex Lindl.) A. Rich & Galeotti			542
Brassavola nodosa (L.) Lindl.	7 January 2004 and 9 July 2004	JB	2
Caularthron bilamellatum (Rchb.f.) R.E. Schultes	22 February 2005	GUA	484
Encyclia adenocarpa (La Llave & Lex.) Schltr.	29 April 2004	JB	60
Encyclia parviflora (Regel) Withner	19 March 2004 and 9 March 2005	JB	59
Encyclia cordigera (Kunth) Dressler	5 March 2004 and 9 March 2005	SD	73
Encyclia selligera (Lindl.) Schltr.	24 February 2004	SD	453
Encyclia bractescens (Lindl.) Hoehne	17 March 2005	PP	465
Epidendrum ciliare L.	7 July 2004 and 10 July 2005	SD	403
Epidendrum lacertinum Lindl.	11 May 2004	SD	343
Epidendrum melistagum, Hágsater	5 July 2005	PP	90
Epidendrum polyanthum Lindl.	10 August 2004	SD	319
Epidendrum stamfordianum Bateman	30 October 2003	SD	94
Epidendrum ramosum Jacq.	6 August 2004 and 7 October 2004	SR and SD	104
Guarianthe aurantiaca (Bateman ex Lindl.) Dressler & W.E. Higgins	28 January 2004 and 11 January 2005	SD	31
Guarianthe skinneri (Bateman) Dressler & W.E. Higgins	20 January 2004 and 11 January 2005	JB and SD	37
Jacquiniella cobanensis (Ames & Schltr.) Dressler	28 March 2004	SD	317

TABLE 1. Continued.

Section 1: 2 continued			
Species	Flowering date	Collection site	Accession number (voucher)
Laelia rubescens Lindl.	3 December 2004 and 30 November 2005	SD	396
Meiracyllium trinasutum Rchb.f.	4 March 2004 and 8 April 2005	SD and EPBD	136
Nageliella purpurea (Lindl.) L.O. Williams	1 July 2004	Y	146
Nidema boothii (Lindl.) Schltr.	23 March 2004 and 15 April 2005	SR	155
Prosthechea baculus (Rchb.f.) W.E. Higgins	23 March 2004 and 9 March 2005	SD	57
Prosthechea chacaoensis (Rchb.f.) W.E. Higgins	10 February 2005 and 9 March 2005	SD	66
Prosthechea chondylobulbon (A. Rich & Galeotti) W.E. Higgins	17 March 2005	PP	449
Prosthechea cochleata (L.) W.E. Higgins	7 July 2004 and 5 July 2005	SD and PP	384
Prosthechea livida (Lindl.) W.E. Higgins	8 August 2005	SD	382
Prosthechea ochracea (Lindl.) W.E. Higgins	10 August 2004 and 13 December 2004	SD	78
Prosthechea radiata (Lindl.) W.E. Higgins	25 June 2004 and 9 July 2004	SR	386
Scaphyglottis crurigera (Bateman ex Lindl.) Ames & Correll	23 March 2004 and 8 March 2005	SD	214
Scaphyglottis sp.	23 October 2005	TG	534

Section 1: 3			
Species	Flowering date	Collection site	Voucher
Tribe Epidendreae			
Subtribe Pleurothallidinae			
Platystele ovatilabia (Ames & C. Schweinf.) Garay	5 March 2005	SD	354
Pleurothallis sp. 1	14 and 17 March 2005	PP	370
Pleurothallis sp.2	27 October 2005	LP	357
Specklinia lateritia (Rchb.f.) Pridgeon & M.W. Chase	10 August 2004	SR	381
Specklinia marginata (Lindl.) Pridgeon & M.W. Chase	19 March 2004 and 8 April 2005	EPBD	352
Specklinia tribuloides (Sw.) Pridgeon & M.W. Chase	13 December 2004	SD	197
Stelis quadrifida (La Llave & Lex.) Solano & Soto Arenas	13 December 2004 and 30 November 2005	SD	195
Stelis sp.	5 March 2005	SD	235
Trichosalpinx blaisdellii (S. Watson) Luer	10 October 2004 and 28 August 2005	SD	243
Tribe Cymbidiae			
Subtribe Oncidiinae			
Brassia verrucosa Lindley	4 May 2004 and 2 May 2005	LP	435
Cuitlauzina convallarioides (Schltr.) Dressler & N. H. Williams	26 January 2005 and 5 March 2005	SD	439
Erycina crista-galli (Rchb.f.) N.H. Williams & M.W. Chase	5 November 2003 and 30 August 2005	SD	299
Ionopsis satyrioides Reichb.f.	17 March 2005	COB-ACH	536
Leochilus labiatus (Sw.) Kuntze	30 November 2005	SD	321
Leochilus oncidioides Knowles & Westc.	30 November 2003	SD	335
Leochilus scriptus (Sw.) Rchb.f.	5 January 2005	JB	398
Leochilus aff. *labiatus*. Purple-leaved*	20 January 2004 and 15 January 2005	JB	323
Lockhartia verrucosa Lindl. ex Rchb.f.	30 November 2005	SD	254

TABLE 1. Continued.

Section 1: 3 continued			
Species	Flowering date	Collection site	Accession number (voucher)
Notylia barkeri Lindl.	7 January 2004	SD	362
Oncidium laeve (Lindl.) Beer	29 April 2004 and 14 April 2005	SR	499
Oncidium ornithorrhynchum Kunth	5 March 2004	SD	356
Oncidium sphacelatum Lindl.	5 March 2004	JB	176
Ornithocephalus tripterus Schltr.	8 July 2004 and 28 August 2005	SD	B
Trichocentrum ascendens (Lindl.) M.W. Chase & N.H. Williams	5 January 2005	JB	160
Trichocentrum candidum Lindl.	2 December 2003	SD	259
Trichocentrum microchilum (Bateman ex Lindl.) M.W. Chase & N.H. Williams	10 August 2004	SN	400
Trichocentrum oerstedii (Rchb.f.) R. Jimenez & Carnevalii	20 January 2004	SD	305
Trichopilia tortilis Lindl.	8 March 2005	SD	385

Section 1: 4			
Species	Flowering date	Collection site	Voucher
Subfamily Cymbidiae			
Tribe Catesinae			
Catasetum integerrimum Hook	4 May 2004 and 28 September 2005	JB	22
Cycnoches egertonianum Bateman	0 August 2005	SRI	C
Cycnoches ventricosum Bateman	25 June 2004 and 10 August 2005	SRI	44
Mormodes lineata Bateman ex Lindl.	5 November 2003 and 3 January 2005	SD and JB	138
Tribe Eulophiinae			
Oeceoclades maculata (Lindl.) Lindl.*	28 August 2005	SRI	498
Tribe Maxillariinae			
Maxillaria parviflora (Poepp. & Endl.) Garay	10 October 2004 and 28 August 2005	SD	255
Maxillaria densa Lindl.	5 January 2005	SD	130
Maxillaria aff. *elatior* (Rchb.f.) Rchb.f.	8 March 2005	SD	D
Maxillaria friedrichsthalii Rchb.f.	23 March 2004 and 9 March 2005	SD	133
Maxillaria hagsateriana Soto Arenas	5 September 2005	SD	288
Maxillaria ringens Rchb.f.	6 July 2005	SR	452
Maxillaria variabilis Bateman ex. Lindl.	30 November 2005	SD	127
Mormolyca ringens (Lindl.) Schltr.	5 November 2003 and 30 November 2005	SD and JB	145
Trigonidium ergotonianum Bateman ex Lindl.	6 April 2004	JB	479
Tribe Stanhopeinae			
Gongora galeata (Lindl.) Rchb.f.	7 July 2004 and 7 July 2005	LP	98
Stanhopea saccata Bateman	7 July 2004	SD	229
Tribe Zygopetilinae			
Kefersteinia tinschertiana (Pupulin)	8 July 2005	LP	E
Subfamily Vandeae			
Tribe Polystachyinae			
Polystachya foliosa (Hook) Rchb.f.	2 September 2004	SD	183
Tribe Angraecinae			
Campylocentrum micranthrum (Lindl.) Rolfe	8 April 2005	EPBD	265

All accession numbers are prefixed by JBSOC-ECOSUR-TAP-MEX.

are managed by the project "Ecology and sustainable cultivation of native orchids" of the Biodiversity Conservation Dept. of ECOSUR, Tapachula. Under these conditions it was not possible to estimate the age of the flower, and it is possible that some pollinaria were older and more dehydrated than others at the time of collection. Date and place of collection of all plants are recorded in a data base.

We studied many more specimens of pollinia than are presented here, but have only included those that can be supported by photographs of the flowers and live specimens of the plants maintained in the Regional Botanic Garden "El Soconusco." All plants are referenced by accession numbers maintained in a data base.

A total of 91 species from 48 genera were included in this study, of which 79 were fully identified. Flowers were placed into inflated, sealed plastic bags with details of plant species, date and locality, and transported to the laboratory in ECOSUR in Tapachula. This study was carried out using the best single sample of a pollinarium for each species; and where there was a second flowering during the study period, a second sample was taken to confirm the characteristics noted.

The classification applied in this study is that of Chase et al. (2003). The taxonomy of a few of the genera is confused. In the case of *Isochilus,* although *I. aurantiacus* is clearly distinguishable, divisions between the other species listed for the Soconusco region, *I. carnosiflorus, I. latibracteatus, I. linearis* and *I. major,* are not so clear. The different samples of pollinia collected from the various *Isochilus* in the area showed notable differences which were not obvious from the flowers. These specimens, tentatively named *I. carnosiflorus, I.* aff. *latibracteatus, I.* aff. *linearis, I.* aff. *major,* and one sample that did not coincide with any of these (*I.* sp.), are included in this study and may prove to be useful for future studies of this genus. *Stelis* is another confusing genus, and only two of the various species found in the Soconusco region are included in this study: one, identified to genus level only; and one species, currently known as *S. quadrifida,* which has a confused taxonomic history (Solano & Soto Arenas 2003a and b).

The pollinarium was extracted from each fresh flower and mounted upon an aluminum stub held in place with conductive carbon tape with double sided adhesive. Observations were carried out under conditions of low vacuum using a SEM Topcon SM 510, at 25–30 kV and 0.1–0.2 mtorr. An image was recorded of the fresh pollinarium. Individual pollinia were taken from each pollinarium and processed in the following manner:

a) The pollinia were left to soak in distilled water for 30–60 min. until completely hydrated, indicated by color and loss of transparency, after which they were soaked for 30 min. in a series of ethanol solutions at 30, 50, 70, 90 and 100% (two changes at 100%) and finally dried at the critical point of CO_2.
b) The dry pollinia were mounted, as before, on the aluminum stub and then covered in a layer of gold-palladium, to a depth of approximately 20 nm, using a Denton Vacuum Desk II.
c) Observations were carried out using the SEM, under high vacuum, 10–15 kV. An image was taken of the fully processed complete pollinarium and a close up of the surface of the exine layer of one of the pollinia.
d) The mounted samples were fractured using fine tweezers and pins, and the newly exposed surface was covered with gold-palladium for observation of the surface of the section, the internal texture of the pollinia, as well as a close up of the tetrads and the exine layer of the internal walls of the tetrads on the surface.

With the program for the acquiring and processing of images, Orion 6.5, of the SEM Topcon SM 510, the length and width of the individual pollinia were measured, both in the fresh and processed state (rehydrated and dried to the critical point of CO_2).

The number of pollinia per pollinarium was described, as well as the shape and form of the individual pollinium, using as a reference the terminology for symmetrical figures (SACDT 1962, Stearn 1966) and examples from Freudenstein and Rasmussen (1996), Stenzel (2000), and Singer and Koehler (2004).

The texture of the pollinium was described after dry fracture and then classified according to the grade of compaction, in agreement with criteria established in the literature (Dressler 1993, Pacini & Hesse 2002, Hesse et al. 1989, cited by Fitzgerald et al. 1994).

The tetrads on the inside of the pollinia were measured (length and width) and the arrangement of the pollen grains within it were described according to the literature (Yeung 1987a, Ackerman & Williams 1981, Stenzel 2000, Faegri & Iversen 1989). The size of the tetrads presented is an average of the measurements of 10 to 15 tetrads taken from the same pollinium, using images augmented 2000 times.

The ornamentation of the exine layer of the external and internal walls of the tetrads on the surface, and the arrangement of the tetrads was described, using as a reference the Manual of Pollen Terminology presented in the Paldat website (Buchner & Weber 2000); table of exine

classification, with examples from Moore et al. (1991); and the palynology glossary (http://www.bio.uu.nl/~palaeo/glossary/glos-lit.htm).

For well represented groups, a summary of pollinaria and pollinia characteristics is given.

Presentation of Results

The results of the measurements and the morphological characterization of the pollinia of the 91 species studied are presented as four taxonomic sections. For each section, the data are presented in TABLES 2: 1–4 as follows:

(^{R}) Indicates that two specimens were studied, either from different plants or from the same plant in different years.

Number of pollinia (per pollinarium). Where the pollen masses presented different sizes, this is indicated by "l" for large and "s" for small.

Size of pollina. Measured in millimeters and represented the length and width of the pollinium. Measurements were made from the SEM images of both fresh and processed pollinia. The number of measurements made depended upon the number of individual pollinium per pollinarium (2, 4, 6, 8) and an average of pollinia size in each state was calculated. Size reported (width and length) in TABLE 2 is an average value of both states. This result is obviously an approximation and was further influenced by the orientation of the image of the sample from which the measurements were taken.

Shape of pollinia. The shape of each pollinium was noted, using the terminology for symmetrical figures (SACDT 1962 and Stearn 1966). Additional notes are presented if there is asymmetry on one side or face of the pollinia, or if the form is irregular.

Caudicle. The texture and presentation of the caudicles are described. Empty spaces in the table indicate that the pollinia do not have a caudicle.

Size of stipe. Averages of the length and the widest part of the stipe are presented in millimeters. Empty spaces in the table indicate that the pollinia do not present a stipe.

Texture. This is an appreciation of the image at 1000× of the pollinium, taken after the transverse cut was made. The following descriptions were applied: *Floury,* for low level of compaction with both the exterior and the interior tetrads having an exine layer; *C. Soft* (compact soft), for pollinia that disintegrate easily when fractured, the tetrads and their arrangement are easy to see; *C. Hard 1* (compact hard texture, type 1), for pollinia that have entire tetrads when fractured—in only a few cases was it possible to determine the arrangement of the pollen grains within the tetrads; *C. Hard 2* (compact hard texture, type 2), for pollinia that do not fracture easily and the walls of the pollen grains within the tetrads almost always break. A thicker wall joining the individual pollen grains may be observed. It was not possible to determine the arrangement of the tetrads in this category.

Some of the pollinia in all categories had collapsed tetrads, and it was not possible to determine their texture.

Size of tetrad. Measurements of the length and width of the tetrads were taken from images at 2000× and are presented in microns. The size reported is the average of the measurements made of 10 to 15 interior tetrads from the same pollinarium.

Shape of tetrad. The arrangement of pollen grains towards the interior of the tetrads is described. Where two different arrangements were observed for the same species, the first mentioned is the most frequent. The term *calymmate* refers to those tetrads in which the pollen grains share a common covering of exine. It was not possible to determine the arrangement of pollinia with hard texture #2, and images of the tetrads for these species are not included.

Surface tetrads. The tetrads at the surface of the pollinia are described as isometric when they have the same arrangement as the tetrads towards the interior of the pollinia, with no elongation. "Slightly elongated" refers to surface tetrads that are linear and slightly stretched in comparison with interior tetrads. Elongated tetrads are approximately twice as long as wide. These arrangements can be observed at 1000× when the pollinia are fractured and include an edge and part of the interior.

Surface exine layer. The main ornamentation of the exine layer of the external walls of the surface tetrads is described. This parameter can be appreciated at 5000×.

Interior exine layer. The ornamentation of the exine layer of the internal walls of the surface tetrads is described. This parameter can be appreciated at 5000×.

Flowering date. The date on which the flower was collected is recorded.

Collection Site

COBACH: Coffee plantation belonging to COBACH school, Santo Domingo, Municipality of Unión Juárez, Chiapas.

TABLE 2:1. Morphological and morphometric characteristics of the pollinia and tetrads of the orchid species studied in section 1.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Width	Shape of pollinia	Caudicle	Texture[c]	Size of tetrad (μm) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Coelia macrostachya	4	0.60	0.56	triangular, deltoid	granular, hyaline mass holding all pollinia together	c. soft	28.9 × 20.0	slightly elongated	rhomboid, tetrahedral	fossulate	fossulate
Deiregyne hemichrea[R]	4	3.62	0.82	cuneate	n.p.[a]	floury	35.8 × 27.3	elongated	rhomboid	reticulate	reticulate
Elleanthus cyanarocephalus	8	0.90	0.45	elliptical, irregular	granular, long, 4 fused caudicles	c. hard 1	24.8 × 19.7	isometric	calymmate	fossulate	fossulate
Isochilus carnosiflorus[R]	4	0.67	0.29	elliptical	granular, long, 4 fused caudicles	c. hard 1	18.5 × 13.5	slightly elongated	calymmate	scabrate to laevigate	laevigate to rugose
Isochilus aff. *latibracteatus*	4	0.51	0.26	elliptical to oblong	granular, long, 2 fused caudicles	c. hard 2	n.d.[b]	isometric	n.d.[b]	scabrate to laevigate	laevigate to rugose
Isochilus aff. *linearis*	4	0.52	0.21	elliptical	granular, long, 4 fused caudicles	c. hard 2	n.d.[b]	isometric	n.d.[b]	scabrate	gemmate
Isochilus aff. *major*	4	0.60	0.26	elliptical	granular, long, 4 fused caudicles	c. hard 1	20.6 × 17.1	slightly elongated	calymmate	laevigate to rugose	laevigate to rugose
Isochilus sp.	4	0.52	0.26	clavate, flattened	granular, long, 4 fused caudicles	c. hard 2	n.d.[b]	isometric	n.d.[b]	laevigate	laevigate
Sarcoglottis sp. 1	4	3.52	0.56	cuneate, open in center	n.p.[a]	floury	34.4 × 26.8	elongated	rhomboid	reticulate	reticulate
Sarcoglottis sp. 2	4	3.82	0.55	cuneate, open in center	n.p.[a]	floury	37.5 × 26.7	elongated	rhomboid	reticulate	reticulate
Ponera striata	4	0.73	0.56	elliptical to oblong, wide	granular, long, 2 fused caudicles	c. soft	18.2 × 13.7	slightly elongated	rhomboid, tetrahedral	laevigate to rugose	laevigate to rugose
Sarcoglottis sceptrodes	4	5.31	0.76	cuneate, open in center	n.p.[a]	floury	42.1 × 36.5	elongated	rhomboid	reticulate	reticulate
Sobralia macrantha	4	2.10	0.67	irregular	n.p.[a]	floury	26.5 × 21.3	isometric	tetrahedral, rhomboid	verrucate	verrucate

[R] Average of two repetitions; [a] not present; [b] not determined; [c] c: compact.

TABLE 2:2. Morphological and morphometric characteristics of the pollinia and tetrads of the orchid species studied in section 2.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Width	Shape of pollinia	Caudicle	Texture[e]	Size of tetrad (μn) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Barkeria obovata[R]	4	0.36	0.31	almost spherical, flattened	granular, long, 2 fused caudicles	c. soft	21.1 × 13.5	tetrahedral	elongated	laevigate	scabrate
Barkeria skinneri	4	0.80	0.63	obovate, wide, flattened	granular, long, simple	c. soft	24.5 × 19.24	calymmate	slightly elongated	laevigate to rugose	scabrate
Brassavola nodosa[R]	4 l[a] 4 s[b] (+8 mini)	1.10 0.70	0.52 0.39	obovate with one straight side	4 granular, long, simple caudicules with one pollinia at each extreme	c. soft	21.4 × 16.4	tetrahedral	slightly elongated	laevigate	scabrate
Caularthron bilamellatum	4	1.19	0.82	elliptical, irregular, flattened	granular, long, 2 fused caudicles	c. soft	17.8 × 16.0	rhomboid	elongated	laevigate	scabrate
Encyclia adenocarpa	4	0.87	0.55	obovate, flattened	granular, long, simple	c. hard 1	16.7 × 12.9	rhomboid, tetrahedral	elongated	laevigate	scabrate
Encyclia parviflora[R]	4	0.98	0.68	obovate, flattened	granular, long, simple	c. hard 1	18.5 × 15.4	rhomboid, square	elongated	laevigate to scabrate	scabrate
Encyclia cordigera[R]	4	1.78	0.95	obovate, flattened	granular, long, simple	c. hard 1	17.4 × 14.3	rhomboid	elongated	laevigate	scabrate
Encyclia selligera	4	1.02	0.54	obovate, flattened	granular, long, simple	collapsed	n.d.[d]	collapsed	slightly elongated	laevigate	scabrate
Encyclia bractescens	4	1.16	0.81	obovate, flattened	granular, long, simple	c. soft	16.5 × 13.7	rhomboid, tetrahedral	isometric	laevigate to scabrate	scabrate
Epidendrum ciliare[R]	4	1.12	0.98	lingulate	granular, long, 2 fused caudicles	c. hard 1	21.3 × 16.8	rhomboid, square	slightly elongated	laevigate to scabrate	scabrate
Epidendrum lacertinum	4	1.17	0.77	lingulate	granular, long, 2 fused caudicles	c. hard 1	25.0 × 17.3	rhomboid	slightly elongated	laevigate	scabrate

TABLE 2:2. Continued.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Width	Shape of pollinia	Caudicle	Texture[e]	Size of tetrad (μn) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Epidendrum melistagum	4	0.81	0.64	obovate, wide, flattened	granular, long, 2 fused caudicles	c. hard 1	19.2 × 15.2	calymmate	slightly elongated	scabrate to laevigate	gemmate
Epidendrum polyanthum	4	0.59	0.36	elliptical to oblong	granular, long, 2 fused caudicles	c. hard 2	n.d.[d]	n.d.[d]	slightly elongated	scabrate to laevigate	scabrate
Epidendrum stamfordianum	2 l[a] 2 s[b]	0.98 0.84	0.39 0.32	falcate, with one straight side	granular, long, 4 fused caudicles	c. hard 1	14.7 × 11.1	calymmate	isometric	scabrate to laevigate	scabrate
Epidendrum ramosum[R]	4	0.36	0.18	elliptical, flattened	granular, hyaline, long, 2 fused caudicles	c. hard 2	n.d.[d]	n.d.[d]	isometric	laevigate	gemmate
Guarianthe aurantiaca[R]	4	0.92	0.64	obovate, flattened	granular, long, simple	c. soft	15.1 × 12.8	tetrahedral, rhomboid	elongated	scabrate to laevigate	scabrate
Guarianthe skinneri[R]	4	1.01	0.62	obovate, flattened	granular, long, simple	c. soft	16.9 × 12.1	rhomboid	elongated	laevigate to scabrate	scabrate
Jacquiniella cobanensis	2	0.54	0.30	elliptical to oblong	very short	c. hard 1	12.1 × 10.1	calymmate	isometric	laevigate to scabrate	laevigate to rugose
Laelia rubescens[R]	4 l[a] 4 s[b]	0.69 0.57	0.59 0.47	elliptical to oblong, wide	granular, long, simple, with a pollinia at each extreme	c. soft	15.2 × 14.3	tetrahedral	slightly elongated	scabrate to laevigate	scabrate
Meiracyclium trinasatum[R]	4 l[a] 4 s[b]	0.86 0.50	0.24 0.27	clavate elongated and falcate, with one straight side	granular, long, 2 fused caudicles	c. soft	14.4 × 11.8	calymmate	isometric	laevigate	scabrate
Nageliella purpurea	4	0.64	0.34	elliptical, irregular	granular, hyaline, long, 2 fused caudicles	c. hard 2	n.d.[d]	n.d.[d]	elongated	laevigate	laevigate
Nidemia boothii[R]	4	0.64	0.44	obovate, flattened	granular, long, 2 fused caudicles	c. soft	17.6 × 13.7	calymmate	slightly elongated	laevigate	scabrate

TABLE 2:2. Continued.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Width	Shape of pollinia	Caudicle	Texture[e]	Size of tetrad (μn) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Prosthechea baculus[R]	4	1.24	0.78	obovate, flattened	granular, long, simple	c. hard 1	15.7 × 11.5	rhomboid, tetrahedral	slightly elongated	laevigate	scabrate
Prosthechea chacaoensis[R]	4	0.93	0.68	obovate, flattened	granular, long, simple	c. soft	18.3 × 14.8	tetrahedral	slightly elongated	scabrate to laevigate	scabrate
Prosthechea chondylobulbon	4	1.83	1.01	obovate, flattened	granular, long, simple	c. hard 1	18.8 × 15.9	tetrahedral, rhomboid	elongated	laevigate to rugose	scabrate
Prosthechea cochleata[R]	4	0.90	0.56	obovate, flattened	granular, long, simple	c. soft	15.2 × 8.7	tetrahedral	slightly elongated	laevigate	scabrate
Prosthechea livida	4	0.50	0.39	obovate, flattened	granular, long, simple	c. soft	14.3 × 10.7	rhomboid, tetrahedral	slightly elongated	laevigate	scabrate
Prosthechea maculata	4	0.48	0.38	obovate, flattened	granular, long, simple	c. hard 1	16.6 × 11.9	calymmate	elongated	laevigate	scabrate
Prosthechea ochracea[R]	4	0.36	0.23	obovate, flattened	granular, long, simple	c. soft	16.0 × 13.4	tetrahedral	isometric	laevigate to rugose	scabrate
Prosthechea radiata[R]	4	0.91	0.65	obovate, flattened	granular, long, simple	c. soft	14.1 × 10.2	tetrahedral, rhomboid	isometric	laevigate	scabrate
Scaphyglottis crurigera[R]	6	0.32	0.35	triangular, deltoide	granular, hyaline, long, simple and thin	c. soft	20.2 × 15.4	calymmate	slightly elongated	scabrate to laevigate	scabrate
Scaphyglottis sp.	2	0.50	0.43	obovate, flattened	n.p.[c]	c. soft	21.9 × 18.9	calymmate	isometric	laevigate	scabrate

[R] Average of two repetitions; [a] large; [b] small; [c] not present; [d] not determined; [e] c.: compact.

TABLE 2:3. Morphological and morphometric characteristics of the pollinia and tetrads of the orchid species studied in section 3.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Width	Shape of pollinia	Size of stipe (mm) length × width	Texture[c]	Size of tetrad (μm) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Brassia verrucosa[R]	2	1.48	0.94	pear-shaped	1.08 × 0.42	c. hard 1	18.0 × 14.5	calymmate	slightly elongated	laevigate	scabrate
Cuitlauzina convallarioides[R]	2	1.12	0.48	pear-shaped	0.40 × 0.35	c. soft	18.7 × 13.8	tetrahedral, rhomboid	slightly elongated	laevigate to scabrate	granulate
Erycina crista-galli[R]	2	0.54	0.37	obovate, with one straight side	1.82 × 0.41	c. hard 1	24.2 × 16.4	calymmate	isometric	laevigate	scabrate
Leochilus labiatus	2	0.63	0.50	elliptical, wide	1.18 × 0.26	c. hard 2	n.d.[b]	n.d.[b]	elongated	perforate	without sculpture
Leochilus oncidioides	2	0.81	0.63	elliptical, wide	1.45 × 0.38	c. hard 2	n.d.[b]	n.d.[b]	elongated	microperforate	granulate
Leochilus scriptus	2	0.81	0.72	spherical	1.19 × 0.50	c. hard 2	n.d.[b]	n.d.[b]	slightly elongated	microperforate	scabrate
Leochilus aff. *labiatus*. Purple-leaved[R]	2	0.51	0.45	spherical	1.10 × 0.29	c. hard 1	15.4 × 11.5	calymmate	slightly elongated	perforate	scabrate
Ionopsis satyrioides	2	0.33	0.30	spherical	0.81 × 0.11	c. hard 2	n.d.[b]	n.d.[b]	isometric	laevigate	granulate
Lockhartia verrucosa	2	0.70	0.31	pear-shaped	n.p.[a]	c. hard 1	12 × 11.2	calymmate	slightly elongated	laevigate to rugose	scabrate
Notylia barkeri	2	0.43	0.26	obovate	1.18 × 0.23	c. hard 2	n.d.[b]	n.d.[b]	slightly elongated	microfoveolate	scabrate
Oncidium laeve[R]	2	1.50	0.81	obovate, with one flat face	1.16 × 0.61	c. hard 1	20.5 × 16.2	rhomboid	slightly elongated	laevigate to rugose	without sculpture
Oncidium ornithorhynchum	2	0.91	0.55	obovate	3.01 × 0.30	c. hard 1	18.2 × 13.0	calymmate	slightly elongated	laevigate	scabrate
Oncidium sphacelatum	2	0.86	0.45	obovate, with one straight side	1.14 × 0.26	c. hard 1	15.6 × 10.7	calymmate	slightly elongated	laevigate	scabrate
Ornithocephalus tripterus[R]	4	0.24	0.18	elliptical, wide	1.97 × 0.30	c. hard 1	23.9 × 18.7	tetrahedral	isometric	perforate	without sculpture

TABLE 2:3. Continued.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Width	Shape of pollinia	Size of stipe (mm) length × width	Texture[c]	Size of tetrad (μm) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Platystele ovatilabia	2	0.10	0.09	spherical	n.p.[a]	n.d.[b]	n.d.[b]	n.d.[b]	n.d.[b]	laevigate	foveolate
Pleurothallis sp. 1	2	0.25	0.21	lenticular	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	isometric	foveolate	foveolate
Pleurothallis sp. 2	2	0.61	0.16	clavate, elongated	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	isometric	laevigate	without sculpture
Specklinia lateritia	2	0.38	0.23	droplet-shaped with one flat face	very short	c. hard 2	n.d.[d]	n.d.[d]	isometric	laevigate to scabrate	without sculpture
Specklinia marginata[R]	2	0.21	0.15	lenticular	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	n.d.[b]	hamulate	without sculpture
Specklinia tribuloides	2	0.31	0.17	lenticular	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	isometric	laevigate to rugose	without sculpture
Stelis quadrifida[R]	2	0.39	0.28	obovate, irregular	n.p.[a]	c. soft	n.d.[b]	n.d.[b]	slightly elongated	laevigate	scabrate
Stelis sp.	2	0.33	0.19	obovate	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	isometric	laevigate	gemmate
Trichocentrum ascendens	2	0.87	0.55	obovate	1.01 × 0.53	c. soft	14.3 × 10.9	rhomboid, tetrahedral	slightly elongated	laevigate to rugose	scabrate
Trichocentrum candidum	2	1.30	0.49	clavate, elongated	1.34 × 0.46	c. hard 2	n.d.[b]	n.d.[b]	elongated	scabrate	scabrate
Trichocentrum microchilum	2	1.18	0.59	obovate, with one flat face	1.44 × 0.30	c. hard 1	20.6 × 14.6	calymmate	elongated	laevigate	scabrate
Trichocentrum oerstedii	2	1.54	0.58	obovate, with one straight side	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	elongated	laevigate	scabrate
Trichosalpinx blaisdellii[R]	2	0.27	0.14	lenticular	n.p.[a]	c. hard 2	n.d.[b]	n.d.[b]	isometric	gemmate	without sculpture
Trichopilia tortilis	2	1.64	0.72	obovoid, with one straight side	1.83 × 0.60	c. hard 1	18.38 × 12.2	calymmate	slightly elongated	fossulate	without sculpture

[R] Average of two repetitions; [a] not present; [b] not determined; [c] compact.

TABLE 2:4. Morphological and morphometric characteristics of the pollinia and tetrads of the orchid species studied in section 4.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Size of pollinia (mm) Width	Shape of pollinia	Size of stipe (mm) length × width	Texture[e]	Size of tetrad (μm) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Campylocentrum micranthum	2	0.16	0.15	spherical	0.35 × 0.09	c. hard 2	n.d.[d]	n.d.[d]	n.d.[d]	laevigate	without sculpture
Cycnoches ergotonianum	2	1.35	1.08	elliptical, wide	1.4 × 0.43	c. hard 2	n.d.[d]	n.d.[d]	isometric	verrucate	verrucate
Cycnoches ventricosum[R]	2	2.10	1.60	elliptical, wide	5.05 × 1.28	c. hard 2	n.d.[d]	n.d.[d]	elongated	laevigate to scabrate	scabrate
Gongora galeata[R]	2	1.64	0.53	elliptical, narrow, flattened	1.79 × 0.32	c. hard 2	n.d.[d]	n.d.[d]	isometric	microfossulate	without sculpture
Kefersteinia tintschertiana	2 l[a] 2 s[b]	1.21 1.02	0.56 0.44	clavate	1.02 × 0.34	c. hard 1	13.8 × 10.8	rhomboid	slightly elongated	laevigate to rugose	without sculpture
Maxillaria conferta[R]	4	0.34	0.22	obovate, irregular	0.33 × 0.12	c. soft	17.2 × 13.0	calymmate	isometric	laevigate	without sculpture
Maxillaria densa	4	0.51	0.35	obovate	0.37 × 0.03	c. soft	13.9 × 10.8	calymmate	isometric	laevigate to rugose	laevigate to rugose
Maxillaria aff. *eliator*	2 l[a] 2 s[b]	1.89 1.64	1.22 1.15	obovate, with one straight side	n.p.[c]	c. soft	29.7 × 21.8	rhomboid, tetrahedral	isometric	laevigate to rugose	laevigate to rugose
Maxillaria friedrichsthalli[R]	2 l[a] 2 s[b]	1.00 1.32	0.54 0.33	elliptical, with one flat face	2.34 × 0.52	c. soft	17.7 × 13.6	tetrahedral	slightly elongated	laevigate to rugose	granulate
Maxillaria hagsateriana	4	0.47	0.39	obovate, wide	n.p.[c]	c. soft	19.1 × 14.1	calymmate	isometric	laevigate	granulate
Maxillaria ringens	2 l[a] 2 s[b]	1.25 0.97	0.40 0.37	elliptical, narrow, with one flat face	n.p.[c]	collapsed	n.d.[d]	n.d.[d]	isometric	laevigate	without sculpture
Maxillaria variabilis[R]	2 l[a] 2 s[b]	1.08 0.91	0.62 0.52	obovate, with one straight side	n.p.[c]	c. soft	18.3 × 14.4	tetrahedral	isometric	laevigate	granulate
Mormodes lineata[R]	2	1.66	0.95	obovate	1.89 × 0.89	c. hard 1	27.9 × 21.7	rhomboid	slightly elongated	laevigate to rugose	granulate
Mormolyca ringens	2 l[a] 2 s[b]	0.92 0.72	0.64 0.53	obovate, with one straight side	n.p.[c]	c. soft	22.1 × 14.9	calymmate	isometric	laevigate	laevigate to rugose
Oeceoclades maculata	2	0.73	0.50	trulloid, wide, with one flat side	0.20 × 0.20	c. soft	28.9 × 25.5	calymmate	isometric	scabrate to laevigate	granulate

TABLE 2:4. Continued.

Orchid species	No. pollinia	Size of pollinia (mm) Length	Size of pollinia (mm) Width	Shape of pollinia	Size of stipe (mm) length × width	Texture[e]	Size of tetrad (μm) length × width	Shape of tetrad	Surface tetrads	Surface exine layer	Interior exine layer
Polystachya foliosa	2	0.30	0.27	spherical	n.p.[c]	c. soft	19.6 × 13.8	calymmate	isometric	laevigate	without sculpture
Stanhopea saccata	2	3.02	0.90	clavate elongated	3.02 × 0.59	c. hard 2	n.d.[d]	n.d.[d]	slightly elongated	microfossulate	without sculpture
Trigonidium ergotonianum	2	0.89	0.36	narrow ellipsoid with one flat face	n.p.[c]	c. hard 2	n.d.[d]	n.d.[d]	isometric	laevigate	laevigate

[R] Average of two repetitions; [a] large; [b] small; [c] not present; [d] not determined; [e] c.: compact.

EPBD: Ejido el Prado, Belisario Domínguez, Municipality of Motozintla. GUA: Guatemala. Confiscated plants, precise collection location unknown, now maintained in the Regional Botanical Garden.

JB: Regional Botanical Garden "El Soconusco," Municipality of Tuzantán, Chiapas. Date and place of collection of all plants are recorded in a data base.

LP: Ejido La Patria, Municipality of Tapachula, Chiapas.

PP: Ejido Piedra Partida, Municipality of Motozintla, Chiapas.

SD: Orchidarium "Santo Domingo," Municipality of Unión Juárez, Chiapas. Date and place of collection of all plants are recorded in a data base.

SN: Sala Nueva, Municipality of Motozintla, Chiapas.

SR: Santa Rosalía, Municipality of Tapachula, Chiapas.

SRI: Santa Rita las Flores, Municipality of Mapastepec, Chiapas.

TG: Tuxtla Gutiérrez airport, Chiapas.

Y: Yajalón, Municipality of Yajalón, Chiapas.

Voucher specimens. Most of the samples of pollinaria were collected from plants established in the Regional Botanical Garden "El Soconusco" and the Orchidarium "Santo Domingo," with a very few samples collected from the orchid galleries in rural communities in Soconusco, other sites in the region and, in one case, confiscated plants. All plants are referenced in the data base of the project "Ecology and Sustainable Cultivation of Native Soconuscan Orchids" and the accession numbers are included in TABLE 1 for reference. Due to the rarity of many species, few are represented in the herbarium of ECOSUR-Tapachula; but we are gradually increasing the number of herbarium specimens, which can be accessed using the same accession numbers.

RESULTS AND DISCUSSION

The results are presented in TABLE 2: 1–4, as explained in "Presentation of results," with an additional brief comparative analysis for groups of species.

Section 1

Subfamily Orchidoideae: Tribe Cranichidea. Subtribe Spiranthinae: *Deiregyne, Sarcoglottis*.

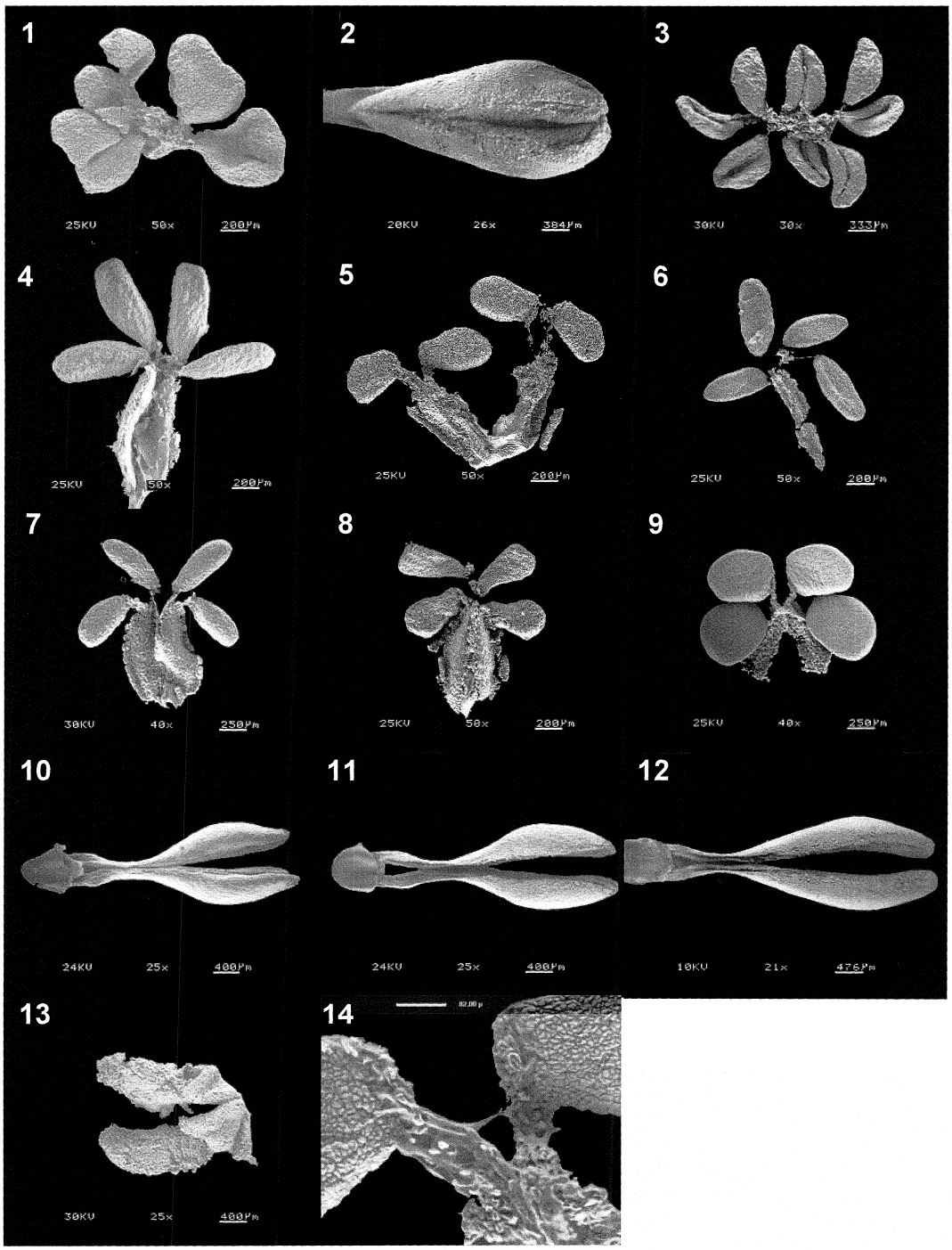

FIGURE 1: 1. Orchids of Soconusco, southeastern Mexico (Tribes Cranichideae, Sobralieae, Ponerinae): Photographs of images taken by a scanning electron microscope of fresh, entire, unprocessed pollinia. Images taken under conditions of low vacuum at 25–30 kV. 1) *Coelia macrostachya,* 2) *Aulosepalum hemichreum,* 3) *Elleanthus cynarocephalus,* 4) *Isochilus carnosiflorus,* 5) *Isochilus* aff. *latibracteatus,* 6) *Isochilus* aff. *linearis,* 7) *Isochilus* aff. *major,* 8) *Isochilus* sp., 9) *Nemaconia striata,* 10) *Sarcoglottis* sp. 1, 11) *Sarcoglottis* sp. 2, 12) *Sarcoglottis sceptrodes,* 13) *Sobralia macrantha,* 14) Close-up of the union between the caudicle and pollinia of *Isochilus* aff. *latibracteatus.*

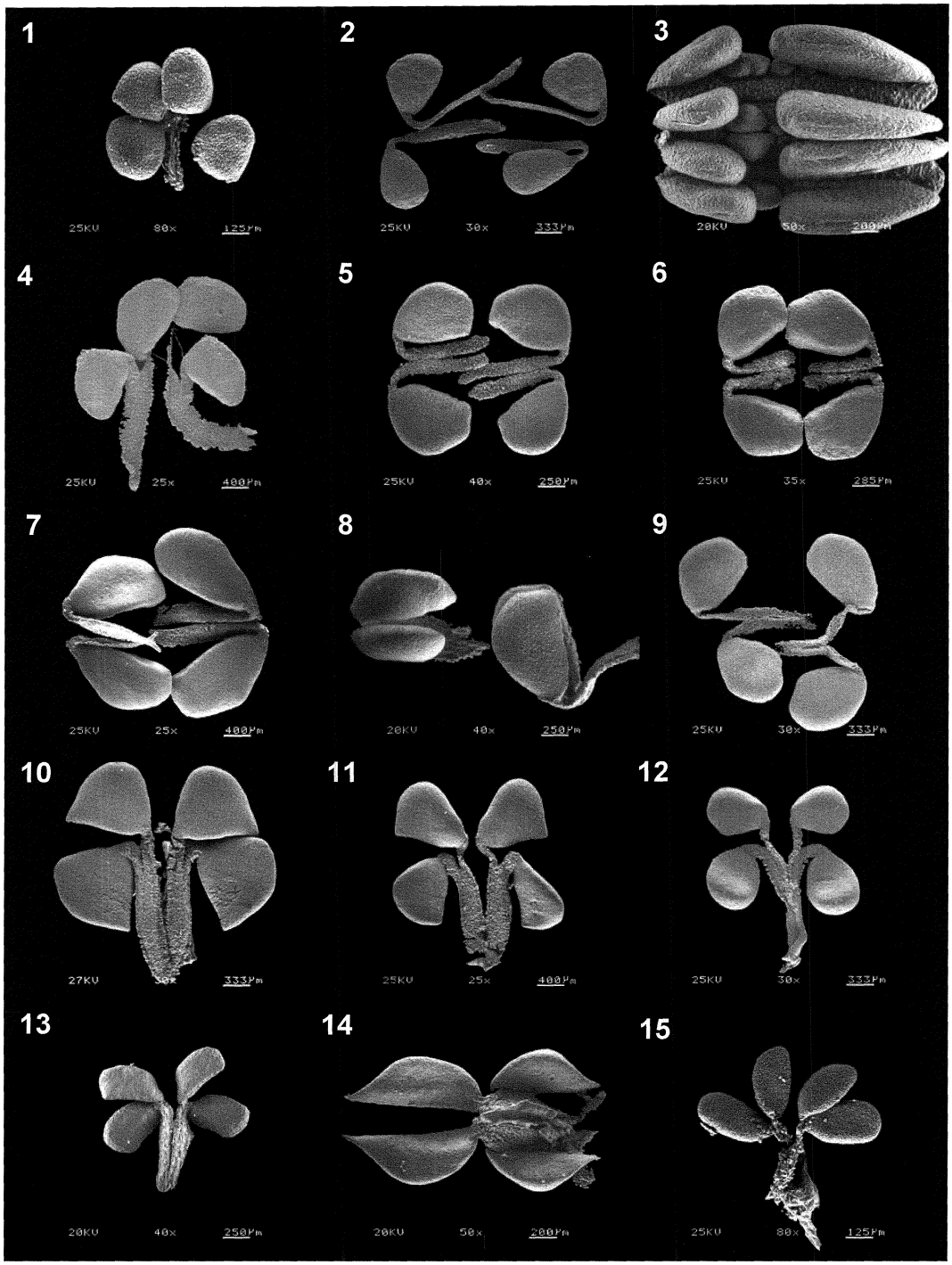

FIGURE 1: 2. Orchids of Soconusco, southeastern Mexico from the subtribe Laeliinae (Tribe Epidendreae): Photographs of images taken by a scanning electron microscope of fresh, entire, unprocessed pollinia. Images taken under conditions of low vacuum at 25–30 kV. 1) *Barkeria obovata,* 2) *Barkeria skinneri,* 3) *Brassavola nodosa,* 4) *Caularthron bilamellatum,* 5) *Encyclia adenocarpa,* 6) *Encyclia parviflora,* 7) *Encyclia cordigera,* 8) *Encyclia selligera,* 9) *Encyclia bractescens,* 10) *Epidendrum ciliare,* 11) *Epidendrum lacertinum,* 12) *Epidendrum melistagum,* 13) *Epidendrum polyanthum,* 14) *Epidendrum stamfordianum,* 15) *Epidendrum ramosum,*

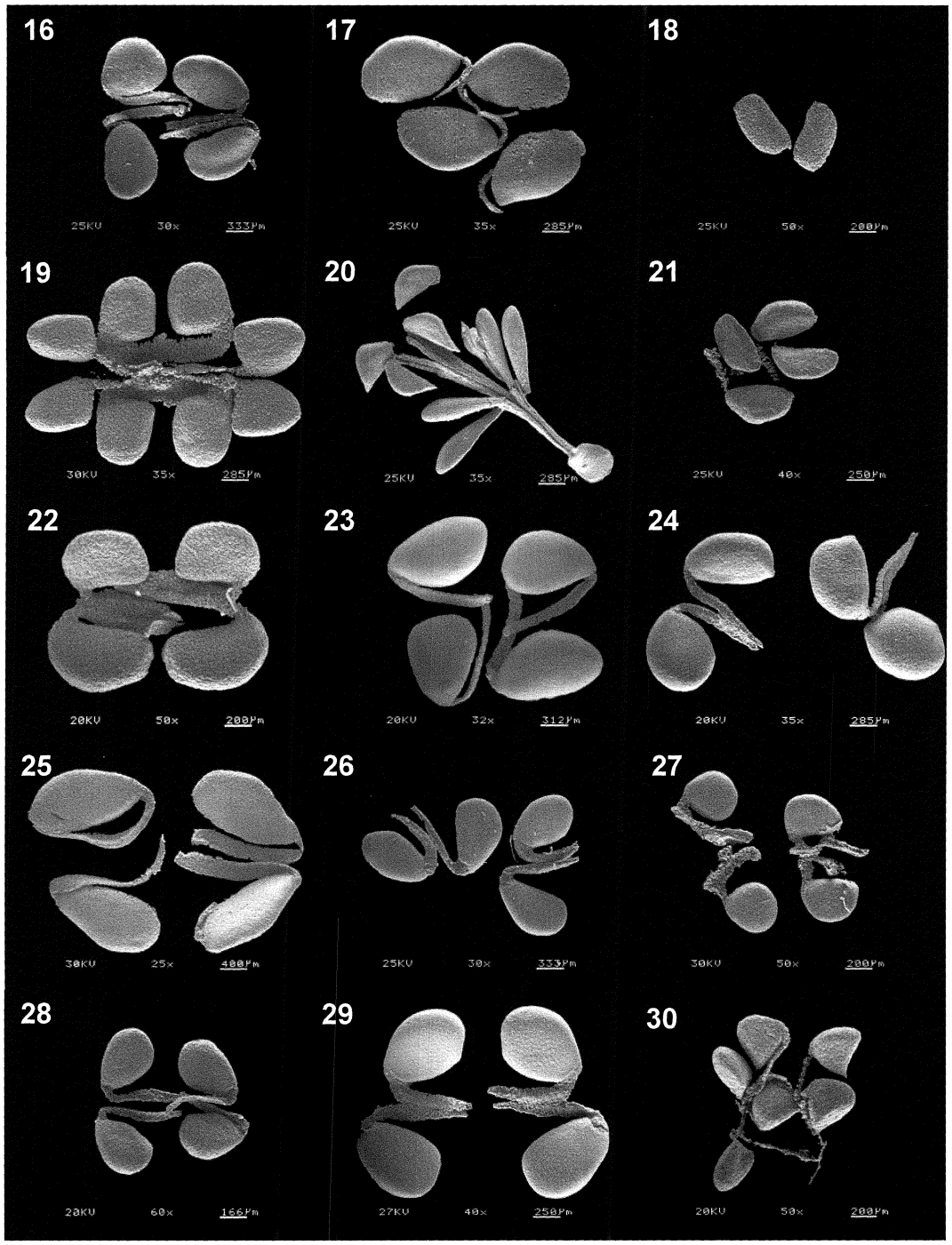

FIGURE 1: 2. (Continued) 16) *Guarianthe aurantiaca,* 17) *Guarianthe skinneri,* 18) *Jacquiniella cobanensis,* 19) *Laelia rubescens,* 20) *Meiracyllium trinasutum,* 21) *Nageliella purpurea,* 22) *Nidema boothii,* 23) *Prosthechea baculus,* 24) *Prosthechea chacaoensis,* 25) *Prosthechea chondylobulbon,* 26) *Prosthechea cochleata,* 27) *Prosthechea livida,* 28) *Prosthechea ochracea,* 29) *Prosthechea radiata,* 30) *Scaphyglottis crurigera,* 31) *Scaphyglottis* sp., 32) Close-up of the union of the caudicle with the pollinia of *Epidendrum ramosum,* 33) Close-up of the caudicle of *Prosthechea cochleata.*

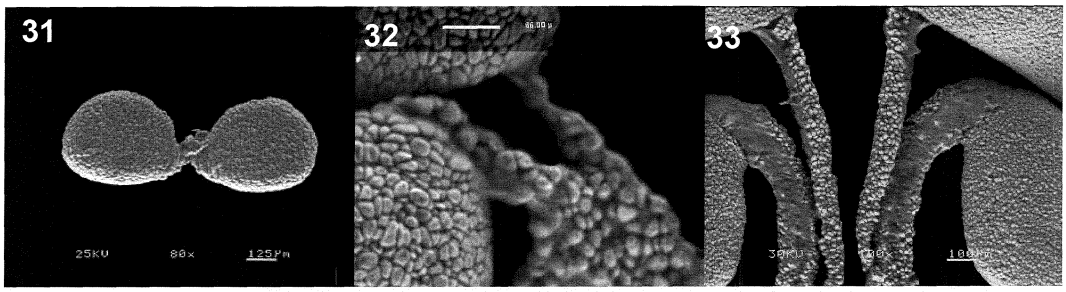

FIGURE 1: 2. Continued.

Subfamily Epidendroideae: Tribe Sobralieae. *Elleanthus, Sobralia*
Subtribe Bletiinae: *Coelia.*
Tribe Epidendreae. Subtribe Ponerinae: *Isochilus, Nemeconia.*

The pollinaria of the species studied have 4 or 8 pollinia with different sizes and forms (TABLE 2:1). Pollinia of species of the Subtribe Spiranthinae are the largest; the 4 pollinia can be distinguished by thin lines along the entire length, which suggests that the 4 pollinia are superposed. However, it is not possible to separate them without causing extensive damage, due to their fragile and floury consistency. The species studied of the Ponerinae possess 4 pollinia and fused, granular caudicles, with 2 or 4 of the caudicles fused together.

Subtribe Spiranthinae

The pollinaria of the four species of this tribe are characterized by having 4 pollinia. The pollinia are cuneate in form, open in the middle for *Sarcoglottis,* and closed for *Aulosepalum.* All the species studied have a viscidium as an accessory structure to facilitate adhesion to the pollinator. *Aulosepalum* and *Sarcoglottis* sp. 1 and 2 have pollinia of a similar size, from 3.52 to 3.82 mm in length by 0.55 to 0.82 mm in width, whereas the pollinia of *Sarcoglottis sceptrodes* measures 5.31 × 0.76 mm, which is the largest of all the pollinia so far studied in Soconusco (see FIGURE 1: 1, Nos. 2, 10–12). All three species have pollinia with a floury texture, and the tetrads separate very easily.

The tetrads of *Aulosepalum* and the two species of *Sarcoglottis* are similar in size, approximately 36 × 27 μm; while, as expected, the tetrads of *Sarcoglottis sceptrodes* are larger, at 42.1 × 36.5 μm. The tetrads of all the species studied are positioned in a rhomboid arrangement (FIGURE 3: 1, Nos. 2, 10–12). The ornamentation of the exine layer is identical for the two species of *Sarcoglottis*; for *Sarcoglottis sceptrodes,* the lumen of the reticulation is more closed and for *Aulosepalum,* more open (FIGURE 4: 1, Nos. 2, 10–12).

Differentiating between the two species of *Sarcoglottis* would be difficult because they have very similar pollinia structures. The only notable difference is in the form of the viscidium: in one species it has the form of an arc and in the other, a "v". The two plants have very different coloring and density of hairs on the leaves and stems, but it is possible that they are, in fact, forms of the same species.

Tribe Sobraliae

The pollinaria of this tribe have 4 or 8 pollinia without well-defined accessory structures; instead they are united by a mass of tetrads engulfed in viscin situated at one extreme of the pollinia. *Elleanthus cynarocephalus* is the only species that has 8, well-separated pollinia (FIGURE 1:1, No. 3). In *Coelia macrostachya* the 4 pollinia are arranged like a four-leaved clover and seem to be only weakly connected (FIGURE 1:1, No. 1). The pollinia of *Sobralia macrantha* are fragile; the tetrads separate easily, and the form is irregular (FIGURE 1:1, No. 10).

The texture of the pollinia of this tribe is variable, from floury, as for *S. macrantha* (FIGURE 2:1, No. 10), soft compact for *C. macrostachya* (FIGURE 2:1, No. 1), to hard compact 1 for *E. cynarocephalus* (FIGURE 2:1, No. 3).

The tetrads are a similar size for all three species (20–28 mm in diameter), and it is possible to determine the arrangement of the individual pollen grains for both *C. macrostachya* and *S. macrantha* (FIGURE 3:1, Nos. 1, 10). However, we classified the tetrads of *E. cynarocephalus* (FIGURE 3:1, No. 3) as calymmate, as they are slightly collapsed and the dividing lines are difficult to see.

The ornamentation of the exine layer of the external and internal walls of the tetrads is similar for all three species: fossulate for *C. macrostachya* and *E. cynarocephalus* (FIGURE 4:1, Nos. 1, 3) and verrucate for *S. macrantha* (FIGURE 4:1, No. 10).

The three species of this tribe are character-

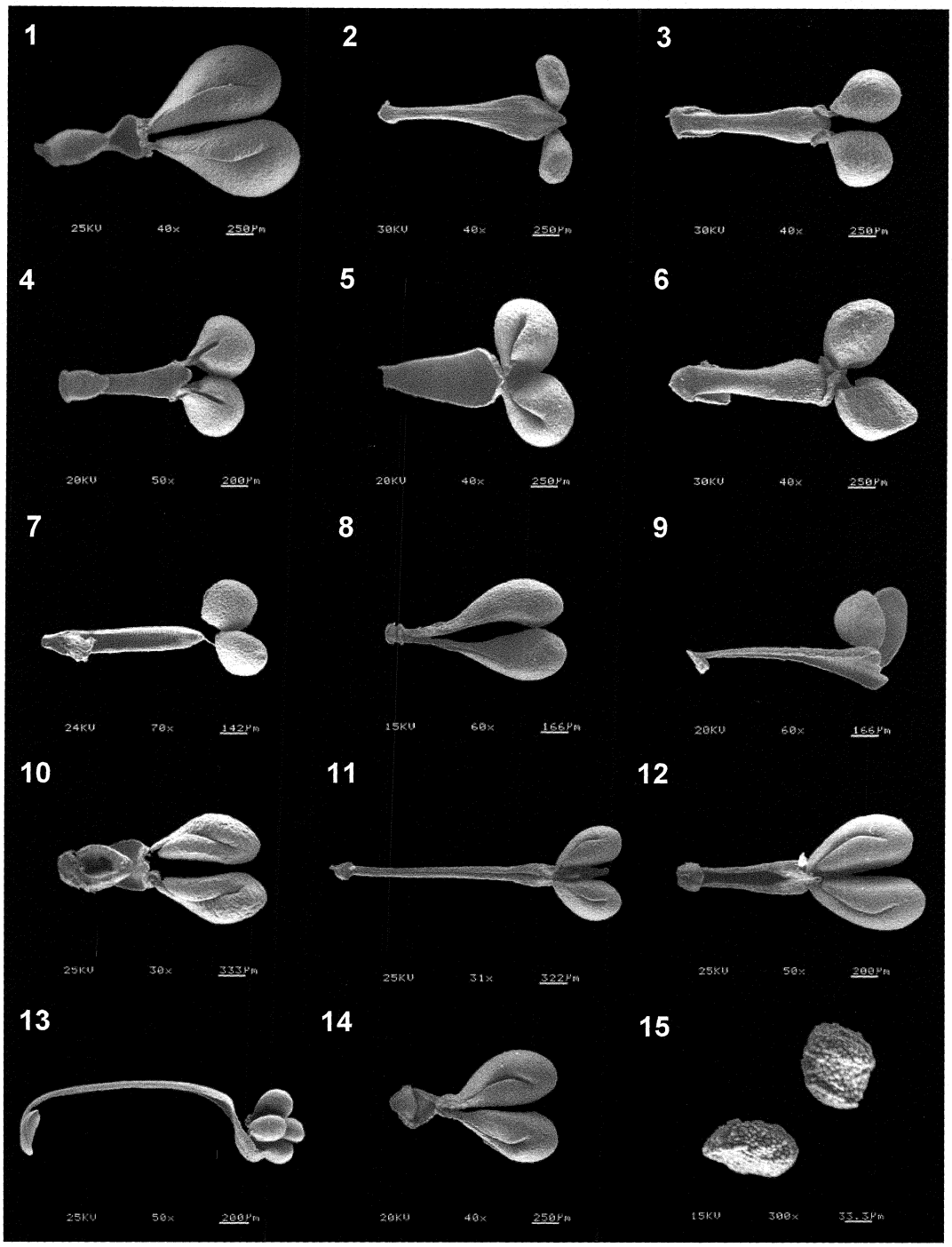

FIGURE 1: 3. Orchids of Soconusco, southeastern Mexico from the Tribe Pleurothallidinae (Subfamily Epidendreae) and Tribe Oncidiinae (Subfamily Cymbidiae): Photographs of images taken by a scanning electron microscope of fresh, entire, unprocessed pollinia. Images taken under conditions of low vacuum at 25–30 kV. 1) *Brassia verrucosa,* 2) *Erycina crista-galli,* 3) *Leochilus labiatus,* 4) *Leochilus* aff. *labiatus,* 5) *Leochilus scriptus,* 6) *Leochilus oncidioides,* 7) *Ionopsis satyrioides,* 8) *Lockhartia verrucosa,* 9) *Notylia barkeri,* 10) *Oncidium laeve,* 11) *Oncidium ornithorrhynchum,* 12) *Oncidium sphacelatum,* 13) *Ornithocephalus tripterus,*

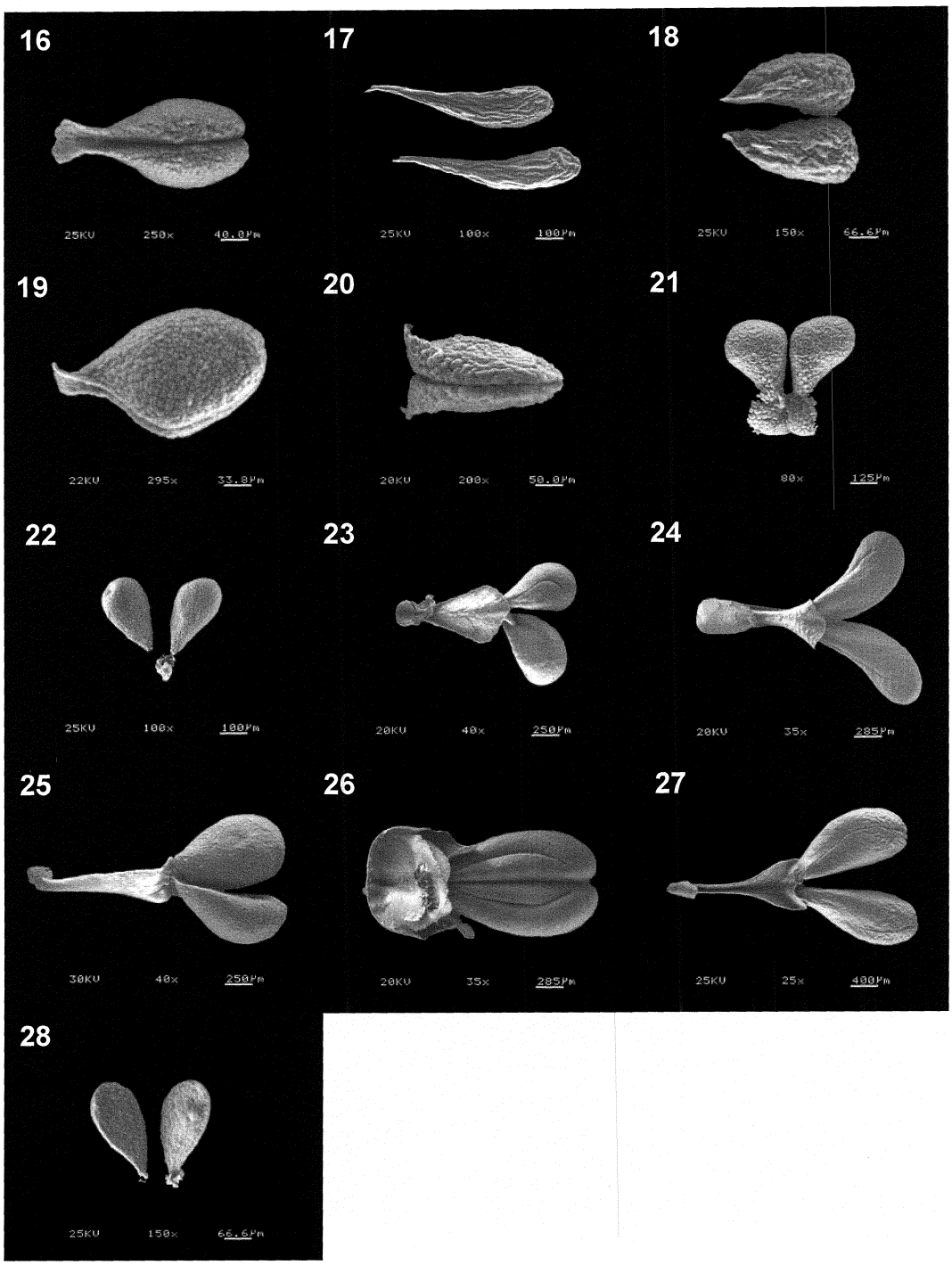

FIGURE 1: 3. (Continued) 14) *Cuitlauzina convallarioides,* 15) *Platystele ovatilabia,* 16) *Pleurothallis* sp. 1, 17) *Pleurothallis* sp. 2, 18) *Specklinia lateritia,* 19) *Specklinia marginata,* 20) *Specklinia tribuloides,* 21) *Stelis quadrifida,* 22) *Stelis* sp., 23) *Trichocentrum ascendens,* 24) *Trichocentrum candidum,* 25) *Trichocentrum microchilum,* 26) *Trichocentrum oerstedii,* 27) *Trichopilia tortilis,* 28) *Trichosalpinx blaisdellii.*

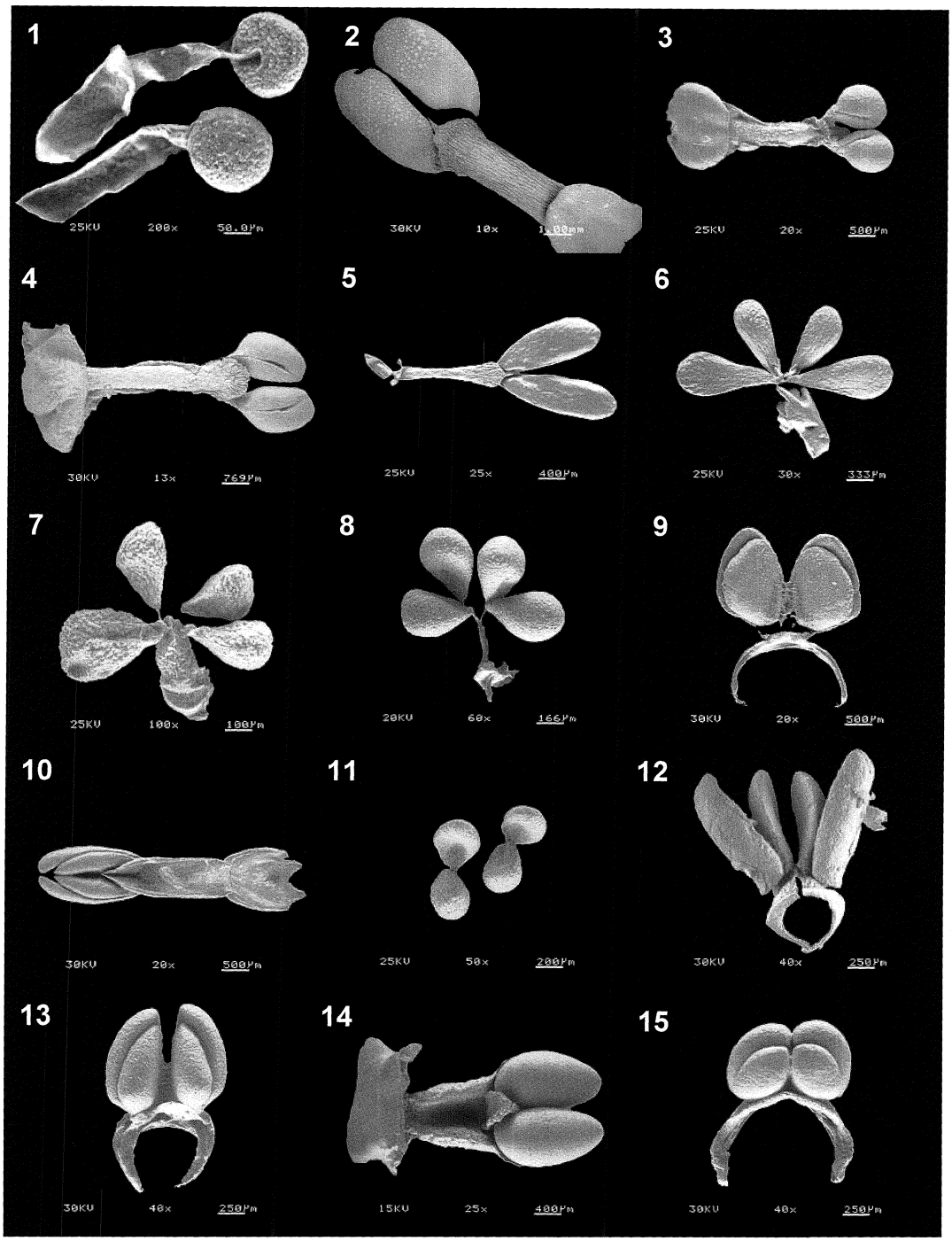

FIGURE 1: 4. Orchids of Soconusco, southeastern Mexico from the Tribes: Catesinae, Eulophiinae, Maxillariinae, Stanhopeinae, Zygopetilinae (Subfamily Cymbidiae) and Tribes: Polystachyinae, Angraecinae (Subfamily Vandeae): Photographs of images taken by a scanning electron microscope of fresh, entire, unprocessed pollinia. Images taken under conditions of low vacuum at 25–30 kV. 1) *Campylocentrum micranthrum,* 2) *Catasetum integerrimum,* 3) *Cycnoches egertonianum,* 4) *Cycnoches ventricosum,* 5) *Gongora galeata,* 6) *Kefersteinia tinschertiana,* 7) *Maxillaria parviflora,* 8) *Maxillaria densa,* 9) *Maxillaria* aff. *elatior,* 10) *Maxillaria*

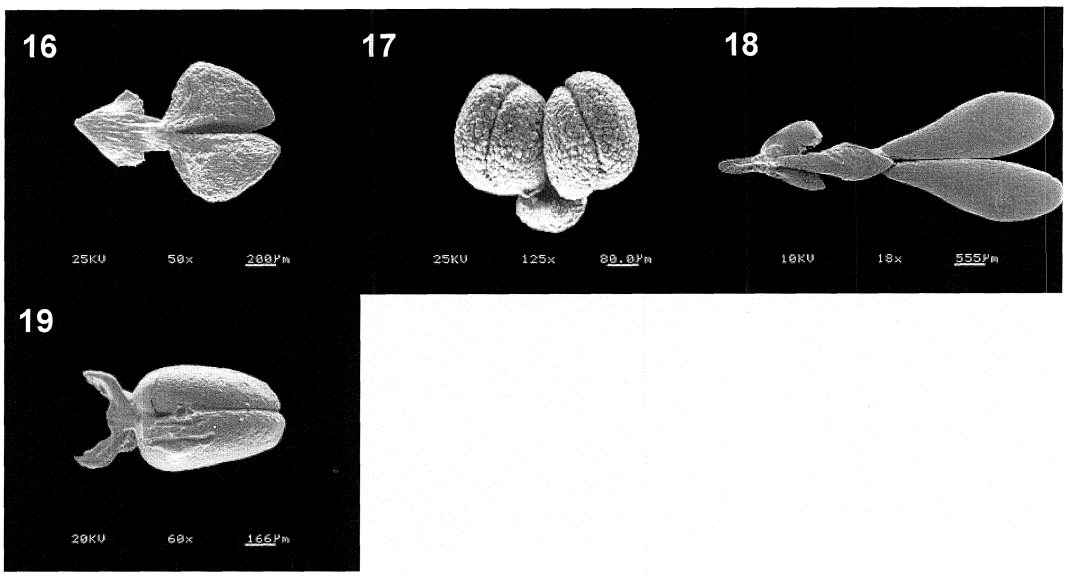

FIGURE 1: 4. (Continued) *friedrichsthalii,* 11) *Maxillaria hagsateriana,* 12) *Maxillaria ringens,* 13) *Maxillaria variabilis,* 14) *Mormodes lineata,* 15) *Mormolyca ringens,* 16) *Oeceoclades maculata,* 17) *Polystachya foliosa,* 18) *Stanhopea saccata,* 19) *Trigonidium ergotonianum.*

ized by having similarly sized tetrads and a well defined ornamentation of the exine layer, which is equal on both surfaces.

Isochilus

The pollinia of *Isochilus* are oval and elongated, with one extreme slightly cut off at the base, in the case of *Isochilus* aff. *latibracteatus* and *Isochilus* sp. (FIGURE 2: 1, Nos. 5, 8). The caudicles are fused with a high viscin content. The size of the pollinia is fairly uniform, with a length of 0.51–0.67 mm and width of 0.21–0.29 mm.

The texture of the pollinia is extremely hard, and when dry-fractured, the walls of the tetrads break open to reveal the cell contents (FIGURE 2: 1, Nos. 4–8). In only two species (*I. carnosiflorus, I.* aff. *major.* FIGURE 3:1, Nos. 4, 5) was it possible to observe entire tetrads, although these are calymmate.

The ornamentation of the exine layer of the external wall of the surface tetrads is laevigate in *I. carnosiflorus, I.* aff. *lactibracteatus* and *I.* aff. *linearis* (FIGURE 4:1, Nos. 4–6); and mainly scabrate in *I.* aff. *major* and *Isochilus* sp. (see FIGURE 4:1, Nos. 7–8). The ornamentation of the internal walls is basically laevigate, with the exception of *Isochilus* aff. *linearis*, which presents a gemmate ornamentation.

Although *Isochilus* and *Nemaconia* belong to the same tribe, they do not share similar characteristics, except for having 4 pollinia per pollinarium. The dominant form for *Isochilus* is elongated elliptical, whereas the pollinia of *Ponera* are wider (FIGURE 1:1, No. 9; FIGURE 2:1, No.9; and FIGURE 3:1, No. 6).

Section 2

Tribe Epidendreae: Subtribe Laeliinae *Barkeria, Brassavola, Caularthron, Encyclia, Epidendrum, Guarianthe, Jacquiniella, Laelia, Meiracyllium, Nageliella, Nidema, Prosthechea, Scaphyglottis.*

Of the approximately 130 native orchid species found up to 1500 m in the region of Soconusco in the southeastern tip of Mexico, 33 belong to Laeliinae. All the species studied are epiphytes, and Laeliinae display a wide range of vegetative and floral morphology and pollination strategies, including examples of all known pollinator groups.

Pollinaria of this sample of Soconuscan orchid species from the subtribe Laeliinae have two to eight, but mostly four pollinia, with a mainly oval or rounded shape. Most pollinia have caudicles, with the exception of *Jacquiniella cobanensis*, often with two or four fused together, and either loosely or firmly attached to the pollinium.

Pollinia are mainly obovate to elliptical and flattened (TABLE 2:2). *Encyclia, Prosthechea, Guarianthe, Brassavola,* some species of *Epidendrum* (*E. ciliare, E. lacertinum*), *Jacquiniel-*

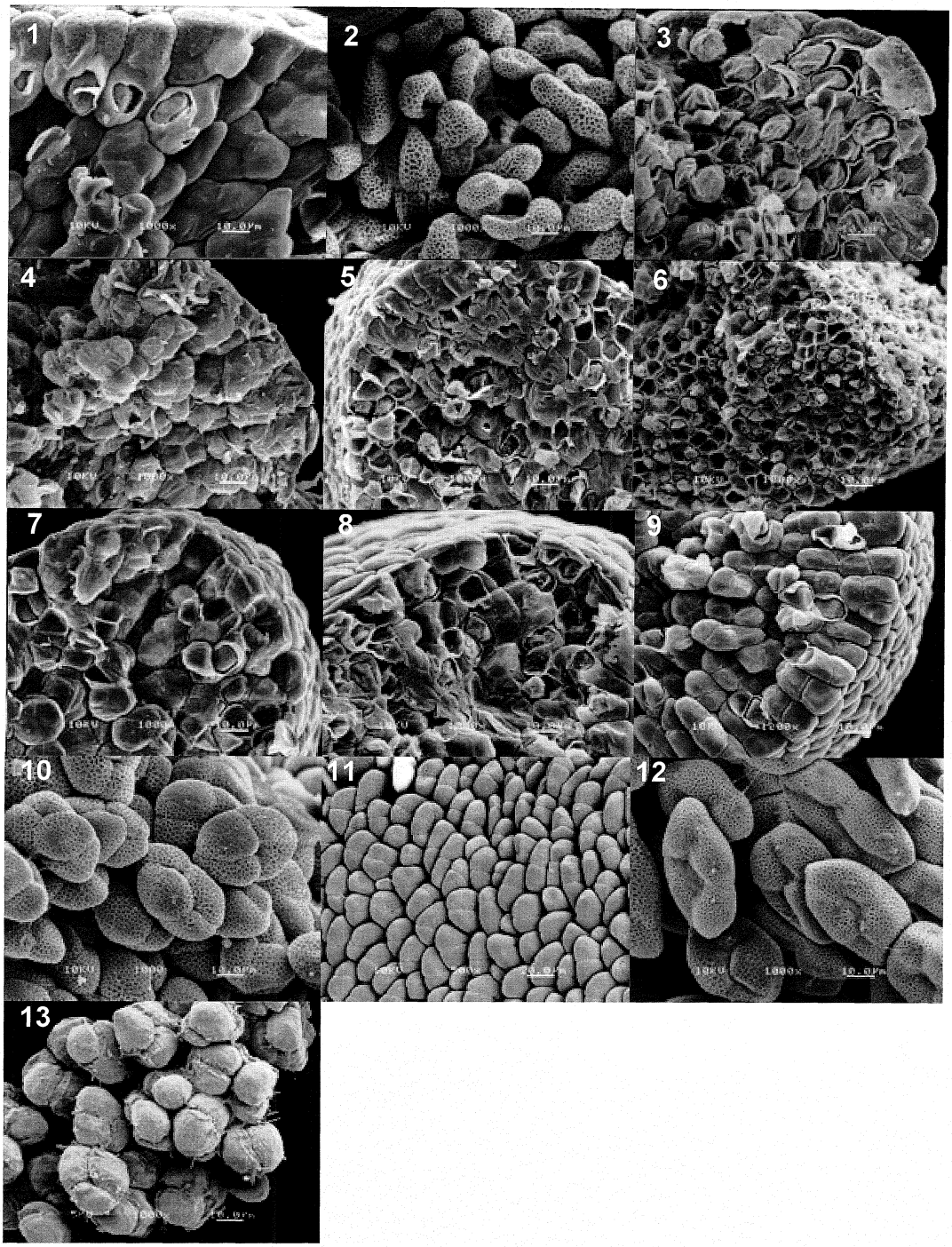

FIGURE 2: 1. Orchids of Soconusco, southeastern Mexico (Tribes Cranichideae, Sobralieae, Ponerinae): Photographs of images taken by a scanning electron microscope of the cut surface of processed and dry-fractured pollinia. Images augmented x 1000 and taken under conditions of high vacuum at 10–15 kV.
1) *Coelia macrostachya,* 2) *Aulosepalum hemichreum,* 3) *Elleanthus cynarocephalus,* 4) *Isochilus carnosiflorus,* 5) *Isochilus* aff. *latibracteatus,* 6) *Isochilus* aff. *linearis,* 7) *Isochilus* aff. *major,* 8) *Isochilus* sp., 9) *Ponera striata,* 10) *Sarcoglottis* sp. 1, 11) *Sarcoglottis* sp. 2, 12) *Sarcoglottis sceptrodes,* 13) *Sobralia macrantha.*

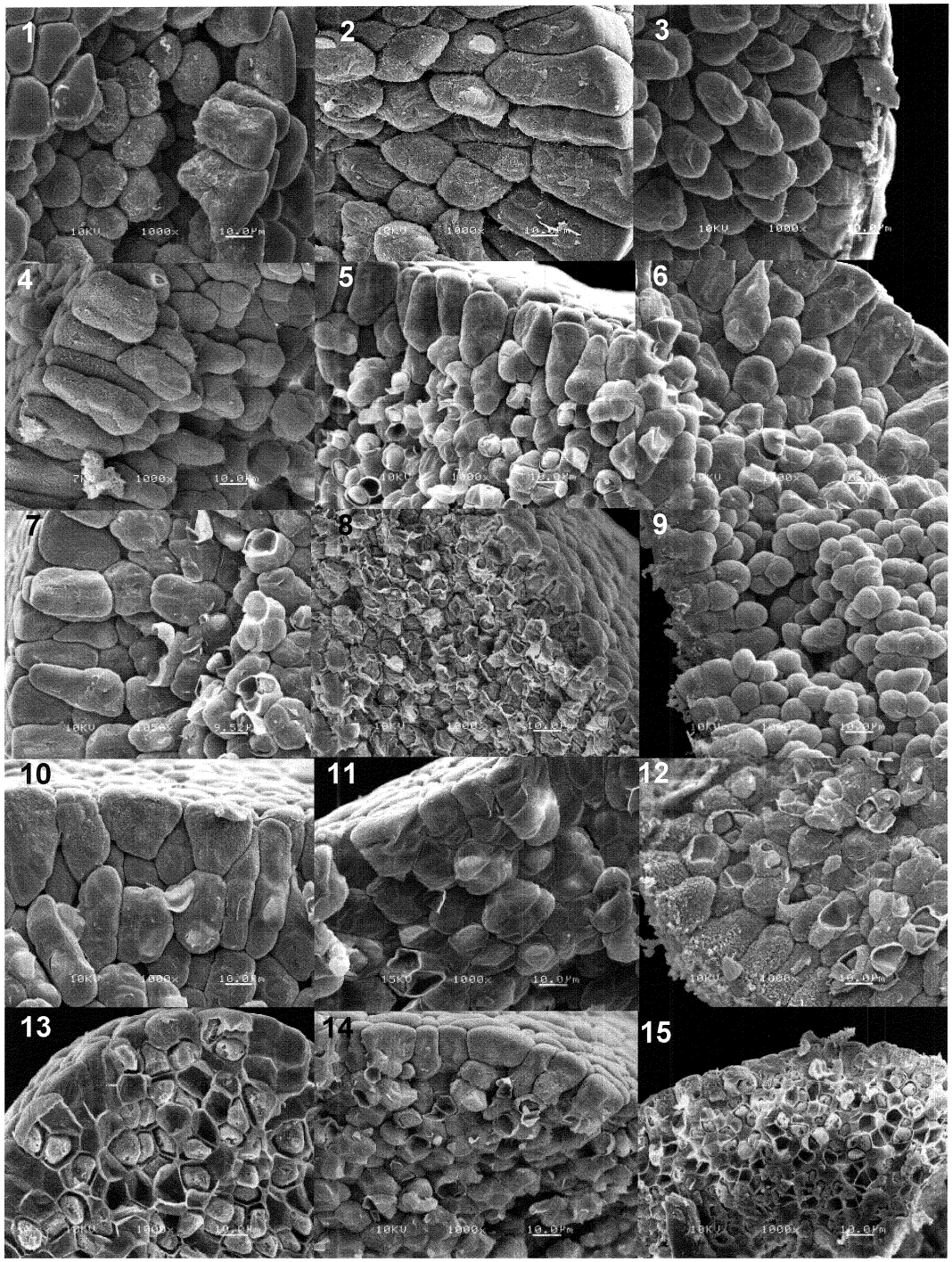

FIGURE 2: 2. Orchids of Soconusco, southeastern Mexico from the subtribe Laeliinae (Tribe Epidendreae): Photographs of images taken by a scanning electron microscope of the cut surface of processed and dry-fractured pollinia. Images augmented x 1000 and taken under conditions of high vacuum at 10–15 kV. 1) *Barkeria obovata,* 2) *Barkeria skinneri,* 3) *Brassavola nodosa,* 4) *Caularthron bilamellatum,* 5) *Encyclia adenocarpa,* 6) *Encyclia parviflora,* 7) *Encyclia cordigera,* 8) *Encyclia selligera,* 9) *Encyclia bractescens,* 10) *Epidendrum ciliare,*

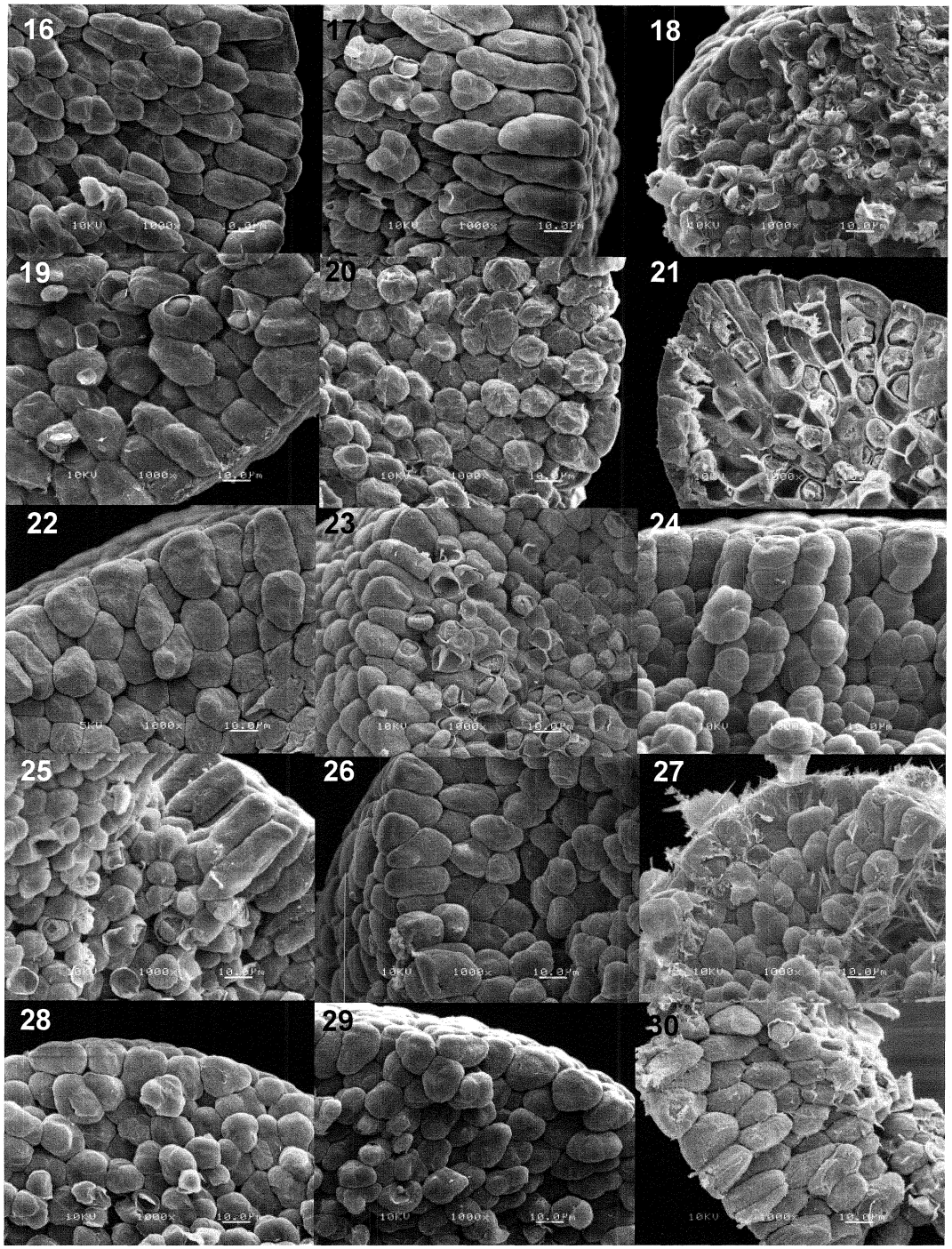

FIGURE 2: 2. (Continued) 11) *Epidendrum lacertinum,* 12) *Epidendrum melistagum,* 13) *Epidendrum polyanthum,* 14) *Epidendrum stamfordianum,* 15) *Epidendrum ramosum,* 16) *Guarianthe aurantiaca,* 17) *Guarianthe skinneri,* 18) *Jacquiniella cobanensis,* 19) *Laelia rubescens,* 20) *Meiracyllium trinasutum,* 21) *Nageliella purpurea,* 22) *Nidema boothii,* 23) *Prosthechea baculus,* 24) *Prosthechea chacaoensis,* 25) *Prosthechea chondylobulbon,* 26) *Prosthechea cochleata,* 27) *Prosthechea livida,* 28) *Prosthechea ochracea,* 29) *Prosthechea radiata,* 30) *Scaphyglottis crurigera,* 31) *Scaphyglottis* sp.

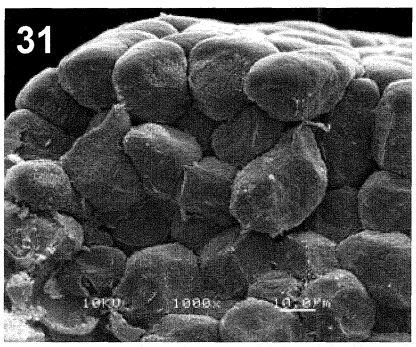

FIGURE 2: 2. Continued.

la, Nageliella and *Nidema* (FIGURE 1: 2, Nos. 10, 11, 18, 21, 22), for example, display the characteristic form, which is obovate with a degree of asymmetry: a straighter side and the other side with a protuberance that resembles a rose petal. Although the most common shape is obovate, there are noticeable differences between the length:width ratios (data not included in TABLE 2:2).

Pollinia of *Epidendrum* (FIGURE 1: 2, Nos. 10–15) are the most varied in shape, from obovate, elliptical and lingulate to falcate (resembling a half-leaf shape, cut longitudinally) examples. Other species had atypical forms such as a flattened sphere (*Barkeria obovata*, *Laelia rubscens,* FIGURE 1: 2, Nos. 1 and 19, respectively), and triangular shapes (*S. crurigera,* FIGURE 1: 2, No. 30).

For all species studied, all the individual pollinia within the pollinarium share the same form, with the exception of *Meiracyllium trinasutum,* which has a combination of falcate to ellipsoidal pollinia (FIGURE 1: 2, No. 20). Furthermore, in most cases the individual pollinia are of a similar size, with the exceptions of *Brassavola nodosa, L. rubescens* (FIGURE 1: 2, Nos. 3 and 19, respectively), *Epidendrum stamfordianum* (FIGURE 1: 2, No. 14) and *Nidema boothii* (FIGURE 1: 2, No. 22), in which the pollinia are divided equally between small and large, as can be inferred from the measurements in TABLE 2:2.

The majority of species had four pollinia per pollinarium, *J. cobanensis* have only two pollinia and *L. rubescens* and *M. trinasutum* have eight (FIGURE 1: 2, Nos. 19 and 20). *B. nodosa* (FIGURE 1: 2, No. 3) represents an extreme case in which as well as four pairs of pollinia united by a common caudicle, there are at least two more small, round pollen masses situated toward one side of the caudicle. Size of the pollinia ranges from 0.3 × 0.2 mm (*B. obovata, Epidendrum ramosum, Prosthechea ochracea,* and *S. crurigera*) to 1.8 × 1.0 mm (*Encyclia cordigera* and *Prosthechea chondylobulbon*).

All of the pollinia in our samples have a caudicle, with the exception of *J. cobanensis* (FIGURE 1: 2, No. 18), in which the caudicle is rudimentary or non-existent and the viscidium is not presented as a cellular structure, rather as an accumulation of viscin or elastoviscin towards one side of the caudicle (FIGURE1: 2, No. 33). Balogh (1982) mentioned that the pollinia of *Jacquiniella* have long caudicles; it is remotely possible that our specimen lost its caudicle within the flower. Variations exist in the granular consistency and the presence of viscin or elastoviscin in the caudicles. Some have compact tetrads with the viscin clearly distinguishable and accumulated towards one side of the caudicle (see FIGURE 1: 2, No. 33), which might facilitate adherence to the pollinator (all species studied of the genera *Brassavola, Encyclia, Guarianthe, Laelia, Nidema* and *Prosthechea* and most species of *Epidendrum*). In all other species the caudicle has more viscin but fewer tetrads, giving a hyaline aspect (*B. obovata, E. ramosum, Nageliella purpurea, S. crurigera*), (FIGURE 1: 2, No. 32). The caudicles can be either easily separated from the pollinia and firmly support them (e.g., all species of *Guarianthe, Encyclia* and *Prosthechea* studied) or be weakly united to the pollinia and with the caudicles of two or four pollinia fused together (*Barkeria, Caularthron, Epidendrum*). Some caudicles are granular and support a pollinium at each extreme, as in *B. nodosa* and *L. rubescens.* In other cases the caudicles are difficult to distinguish because they are fused with the lobes of pollinia that extend towards one side, as in *M. trinasutum.*

The results of the morphological and morphometric analyses of the arrangement of the surface tetrads and the size and texture of the interior tetrads, as seen when fractured, are presented in TABLE 2: 2. The tetrads at the surface of the pollinium in most cases have the same arrangement as the tetrads toward the inside, but with a certain degree of deformation. In some cases, such as *Epidendrum ciliare* and *N. boothii* (FIGURE 2: 2, Nos. 10 and 22) they take on an inverted pyramid shape (like teeth), in which the widest base faces toward the exterior and the narrowest base towards the interior. Other exterior tetrads tend to be arranged in rows in palisade form, forming an external layer distinct to the tetrads on the inside, as in *Caularthron bilamellatum, E. cordigera,* and *Guarianthe skinneri* (FIGURE 2: 2, Nos. 4, 7 and 17, respectively). Only in the case of *N. purpurea* and *P. chondylobulbon* (FIGURE 2: 2, Nos. 21 and 25,

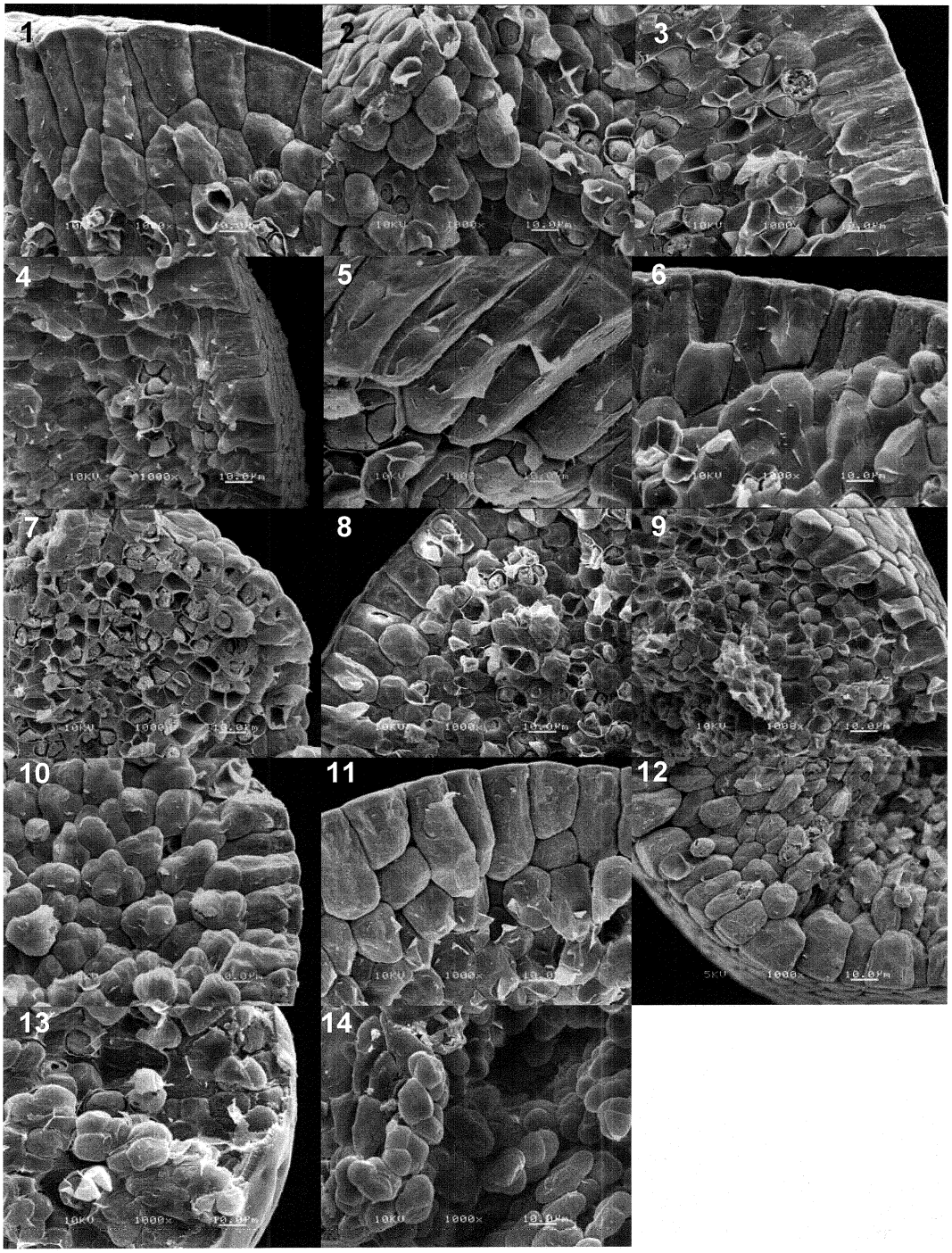

Figure 2: 3. Orchids of Soconusco, southeastern Mexico from the Tribe Pleurothallidinae (Subfamily Epidendreae) and Tribe Oncidiinae (Subfamily Cymbidiae): Photographs of images taken by a scanning electron microscope of the cut surface of processed and dry-fractured pollinia. Images augmented x 1000 and taken under conditions of high vacuum at 10–15 kV. 1) *Brassia verrucosa,* 2) *Erycina crista-galli,* 3) *Leochilus labiatus,* 4) *Leochilus* aff. *labiatus,* 5) *Leochilus scriptus,* 6) *Leochilus oncidioides,* 7) *Ionopsis satyrioides,* 8) *Lockhartia verrucosa,* 9) *Notylia barkeri,* 10) *Oncidium laeve,* 11) *Oncidium ornithorrhynchum,* 12) *Oncidium*

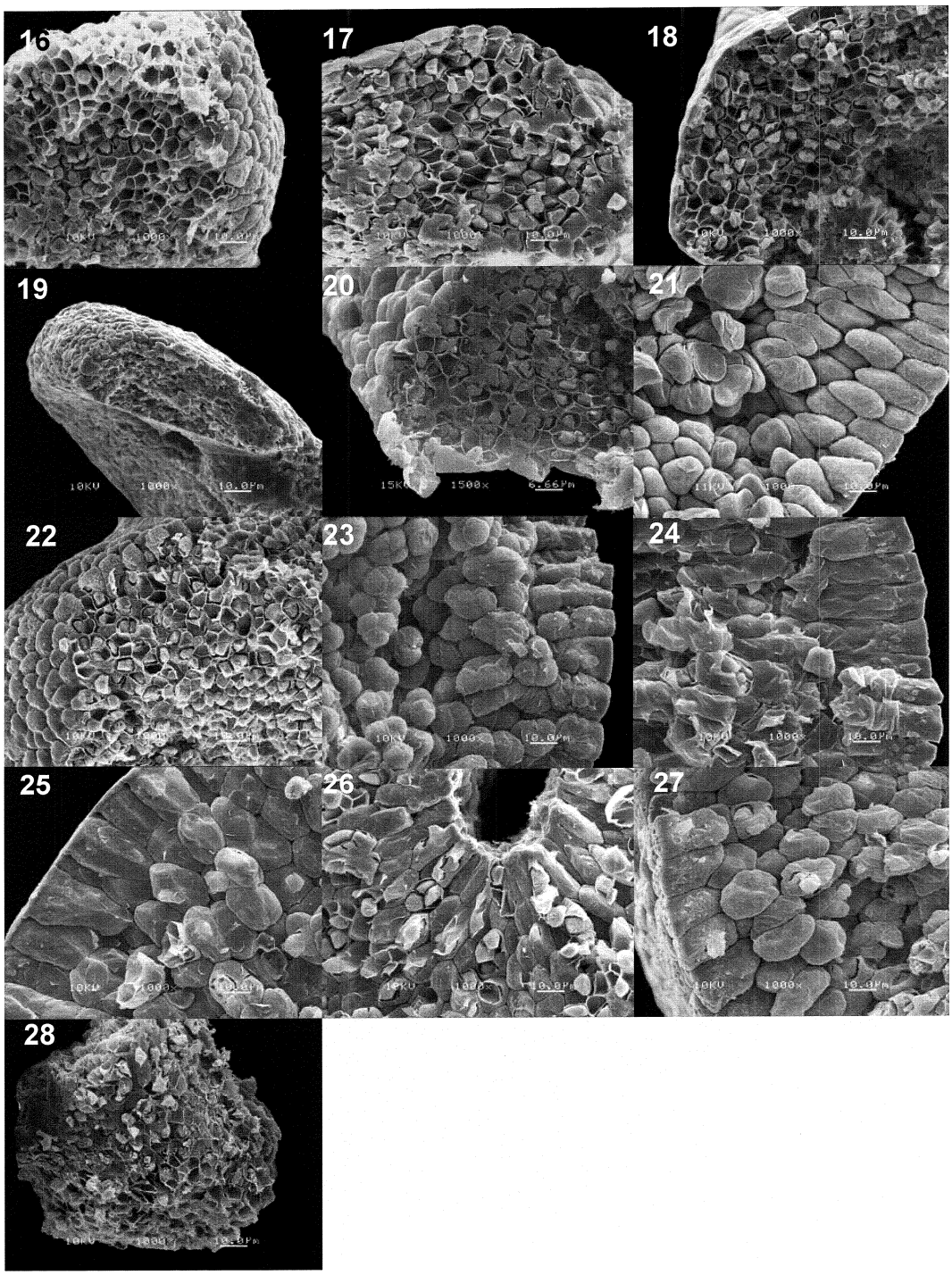

Figure 2: 3. (Continued) *sphacelatum,* 13) *Ornithocephalus tripterus,* 14) *Cuitlauzina convallarioides,* 16) *Pleurothallis* sp. 1, 17) *Pleurothallis* sp. 2, 18) *Specklinia lateritia,* 19) *Specklinia marginata,* 20) *Specklinia tribuloides,* 21) *Stelis quadrifida,* 22) *Stelis* sp., 23) *Trichocentrum ascendens,* 24) *Trichocentrum candidum,* 25) *Trichocentrum microchilum,* 26) *Trichocentrum oerstedii,* 27) *Trichopilia tortilis,* 28) *Trichosalpinx blaisdellii.*

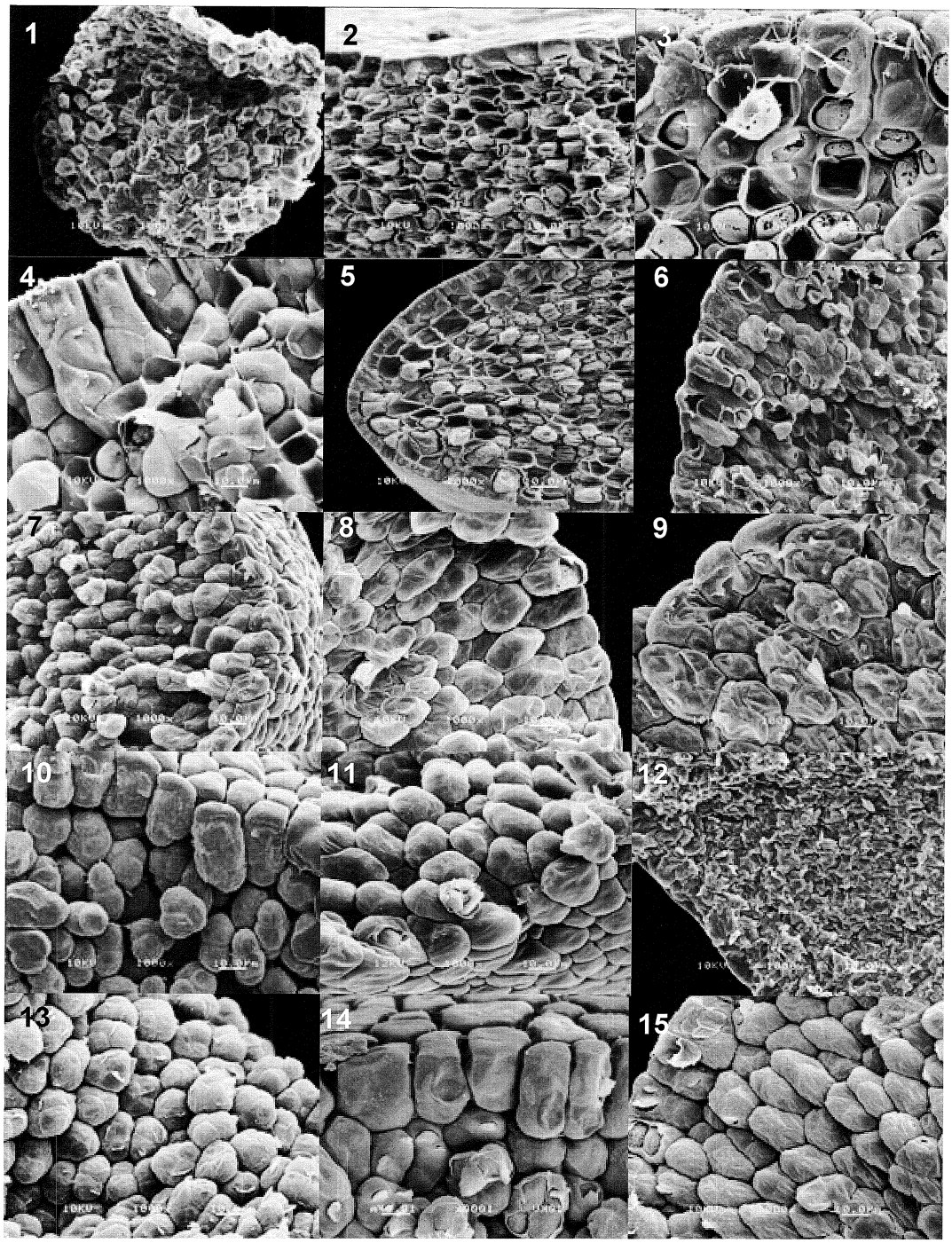

FIGURE 2: 4. Orchids of Soconusco, southeastern Mexico from the Tribes: Catesinae, Eulophiinae, Maxillariinae, Stanhopeinae, Zygopetilinae (Subfamily Cymbidiae) and Tribes: Polystachyinae, Angraecinae (Subfamily Vandeae): Photographs of images taken by a scanning electron microscope of the cut surface of processed and dry-fractured pollinia. Images augmented x 1000 and taken under conditions of high vacuum at 10–15 kV. 1) *Campylocentrum micranthrum,* 2) *Catasetum integerrimum,* 3) *Cycnoches egertonianum,* 4) *Cycnoches ventricosum,* 5) *Gongora galeata,* 6) *Kefersteinia tinschertiana,* 7) *Maxillaria parviflora,* 8) *Maxillaria densa,*

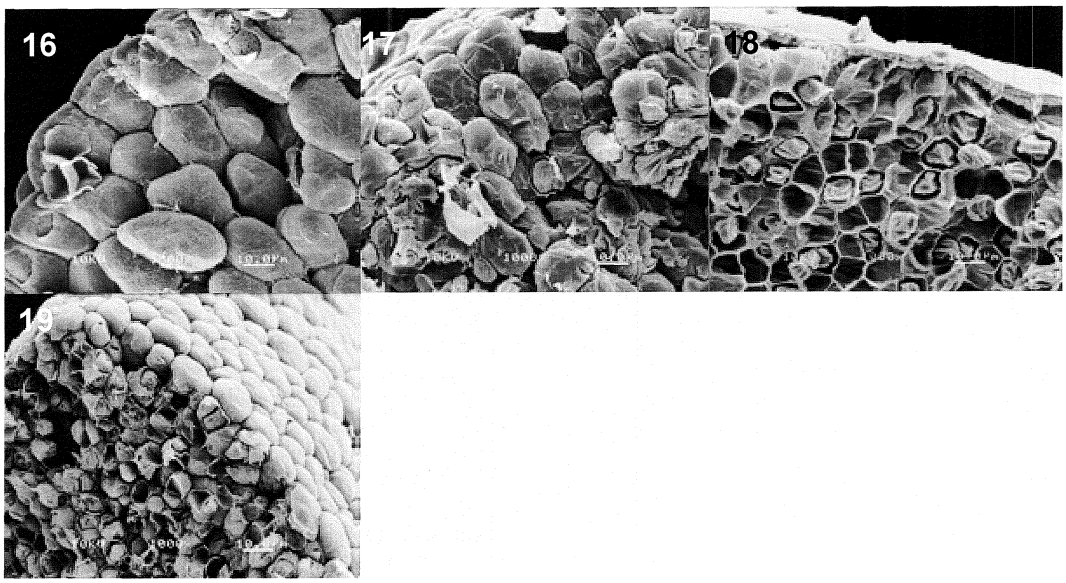

FIGURE 2: 4. (Continued) 9) *Maxillaria* aff. *elatior,* 10) *Maxillaria friedrichsthalli,* 11) *Maxillaria hagsateriana,* 12) *Maxillaria ringens,* 13) *Maxillaria variabilis,* 14) *Mormodes lineata,* 15) *Mormolyca ringens,* 16) *Oeceoclades maculata,* 17) *Polystachya foliosa,* 18) *Stanhopea saccata,* 19) *Trigonidium ergotonianum.*

respectively) are the four pollen grains clearly aligned one behind the other.

Pollinia with a soft, compact texture are easily fractured and have entire tetrads that separate easily (e.g., FIGURE 2: 2, Nos. 1–3), whereas pollinia with a hard compact texture are resistant to fracture, their tetrads do not disintegrate easily, and the walls of the pollen grains tend to break open when doing so, exposing the cell contents (e.g., FIGURE 2: 2, Nos. 10–15). The category of hard compact texture was then subdivided into two: hard compact 1, in which, when fractured, the majority of the tetrads remained entire (e.g., *Encyclia adenocarpa, E. parviflora* and *E. cordigera,* see FIGURE 2:3, Nos. 5–7); and hard compact 2 in which the majority of the tetrads break up, making it impossible to measure and determine the arrangement (e.g., *Epidendrum poyianthum* and *E. ramosum.* FIGURE 2:2, Nos. 13, 15). Given the lack of duplicates in many cases, it was not possible to determine the texture and arrangement of the tetrads of some species (*Encyclia selligera,* among others) that did not rehydrate sufficiently and had a collapsed appearance.

For those pollinia with tetrads that remain intact after fracture, sizes ranged from 25 × 14 to 12 × 10 μm, and no relationship was found between the size of the pollinium and the size of the tetrad. FIGURE 3: 2 shows the tetrads of those species that remained intact. The arrangement of the majority of the tetrads toward the interior of the pollinia is tetrahedral, multiplanar, decussate, or uniplanar and rhomboidal (e.g., FIGURE 3: 2, Nos. 3, 4, 15, 21); and there are examples of pollinia with two types of arrangements (e.g., FIGURE 3: 2, Nos. 6, 9 and 14). In some species the tetrads are calymmate and wrapped in a continuous covering like a bag, which makes it impossible to assess the arrangement of the tetrads (e.g., FIGURE 3: 2, Nos. 13 and 19).

TABLE 2:2 also summarizes the characteristics of the exine layer of the exterior tetrads; the ornamentation of the exterior and interior walls is described separately, and both walls can be appreciated in FIGURE 4: 2. The ornamentation of the majority of the species of this subtribe is laevigate or psilate (*Barkeria,* some *Encyclia, Guarianthe, Prosthechea,* among others. FIGURE 4: 2), although some tetrads have a scabrate surface (*Epidendrum melistagum,* and *P. chacaoensis.* FIGURE 4: 2, Nos. 12 and 24, respectively).

Internal walls of the surface tetrads of the majority of species have a granulated or scabrate ornamentation with the exception of *E. melistagum* and *E. ramosum,* which have a roughly granulate ornamentation and were classified as gemmate (FIGURE 4: 2, No. 12 and 15, respectively).

Guarianthe

Pollinia of both species studied are very similar in size and shape, although the length:width ratio is greater (1.63, data not presented) for *G. skinneri* than for *G. aurantiaca* (1.44, data not

presented). The size of the tetrads is similar, but *G. aurantiaca* can be distinguished by having two different arrangements of the interior tetrads. Their textures are similar, but there are slight differences in the ornamentation of the exine layer of the external wall of the tetrads: whereas *G. skinneri* is laevigate, or smooth, *G. aurantiaca* is slightly scabrate.

Encyclia and *Prosthechea*

The shape and structure of the caudicle are distinctive for these two groups. The size of the pollinia is highly variable, within the range 0.5 × 0.4 to 1.8 × 1.0 mm, with the exception of *P. ochracea* that has exceptionally small pollinia measuring 0.36 × 0.23 mm. The texture of the pollinia is also variable, from soft compact (*P. chacaoensis*) to hard compact 1 (*E. adenocarpa, P. baculus*).

In the majority of cases it is possible to distinguish the four pollen grains of each tetrad and their arrangement, which is usually rhomboid for *Encyclia* and tetrahedral for *Prosthechea*; although some species have two arrangements, both tetrahedral and rhomboidal (*Encyclia.* sp. and *P. livida,* FIGURE 3:2, Nos. 9 and 24, respectively). Size of the tetrads towards the interior of the pollinium is variable, from 14.0 × 10.0 to18.8 × 15.9 μm. The majority of the tetrads at the surface of the pollinium are elongated and palisade in form, with the exception of *P. ochracea* and *P. radiata*, which have isometric tetrads similar to the interior tetrads.

The ornamentation of the external surface of the exine layer is basically laevigate, with different grades of rugosity. The surface tetrads and their internal walls are granular to scabrate.

Epidendrum

Pollinia in *Epidendrum* are variable in shape, and only two of the species studied have a similar form (*E. ciliare* and *E. lacertinum*); the other species have elliptical, obovate or falcate pollinia. Size of the pollinia varies from approximately 0.36 to 1.00 mm and their texture is hard. *E. polyanthum* and *E. ramosum* have fractures in the walls of the majority of the pollen grains, indicating a very high level of cohesion or even fusion of the tetrads.

The shape of the caudicle is consistent for most species, with a granular consistency but a high viscin content (FIGURE 1: 2, No. 33). Either two or four of the caudicles are fused, and these are weakly attached to the pollinium.

The *Epidendrum* species studied have interior tetrads encased in a common covering of unornamented exine (i.e. calymmate), and in the cases of *E. ciliare* and *E. lacertinum,* despite the covering, a thin dividing line can be distinguished between the individual pollen grains enabling the arrangement to be described. The ornamentation of the exine layer of the external walls of the tetrads on the surface ranges from laevigate, with different grades of rugosity, to scabrate; whereas the ornamentation of the internal walls of these tetrads is usually scabrate, but particularly so for *E. ramosum* and *E. melistagum,* which are gemmate.

With respect to the number of pollinia reported in this tribe, Dressler (1993) affirmed that the ancestral number is eight and that from there, there were independent reductions to six, four or two pollinia, indicating that the pollinaria of *B. nodosa, L. rubescens* and *M. trinasutum* are the least evolved within Laeliinae in the Soconusco region. However, according to Freudenstein and Rasmussen (1996), the pollinaria reported here with eight pollinia, as for *B. nodosa*, in reality correspond to four pollinia that are profoundly lobed and united by an unmodified pollen mass. However, we report the appearance of the complete, intact pollinarium; it is not possible to evaluate the interpretation of Freudenstein and Rasmussen without separating or opening the pollinarium.

Compact texture, as well as being related to the level of evolution of the orchid species in question, may also imply the ease with which the tetrads disintegrate, allowing greater freedom for the individual pollen grains to germinate and for the pollen tube to reach the ovules of the receptor flower. Various biological and abiotic factors may be involved, and these characteristics require further study.

The results show marked consistency in the number and form of the pollinia within and between the genera of the Laeliinae in the Soconusco region, with the exception of *Epidendrum*, which displays greater variation. However, although individual species have characteristics that clearly distinguish them, it was not possible to determine characteristics that unite species at the generic level.

Section 3

Tribe Epidendreae. Subtribe Pleurothallidinae: *Platystele, Pleurothallis, Specklinia, Stelis, Trichosalpinx*

Tribe Cymbidiae. Subtribe Oncidiinae: *Brassia, Erycina, Ionopsis, Leochilus, Lockhartia, Notylia, Oncidium, Ornithocephalus, Cuitlauzina, Trichocentrum, Trichopilia*

All the species studied of the subfamily Epidendreae and Cymbidiae have two pollinia, with the exception of *Ornithocephalus tripterus*, which has four well-defined pollinia. Although there are few orchids from Soconusco that fall

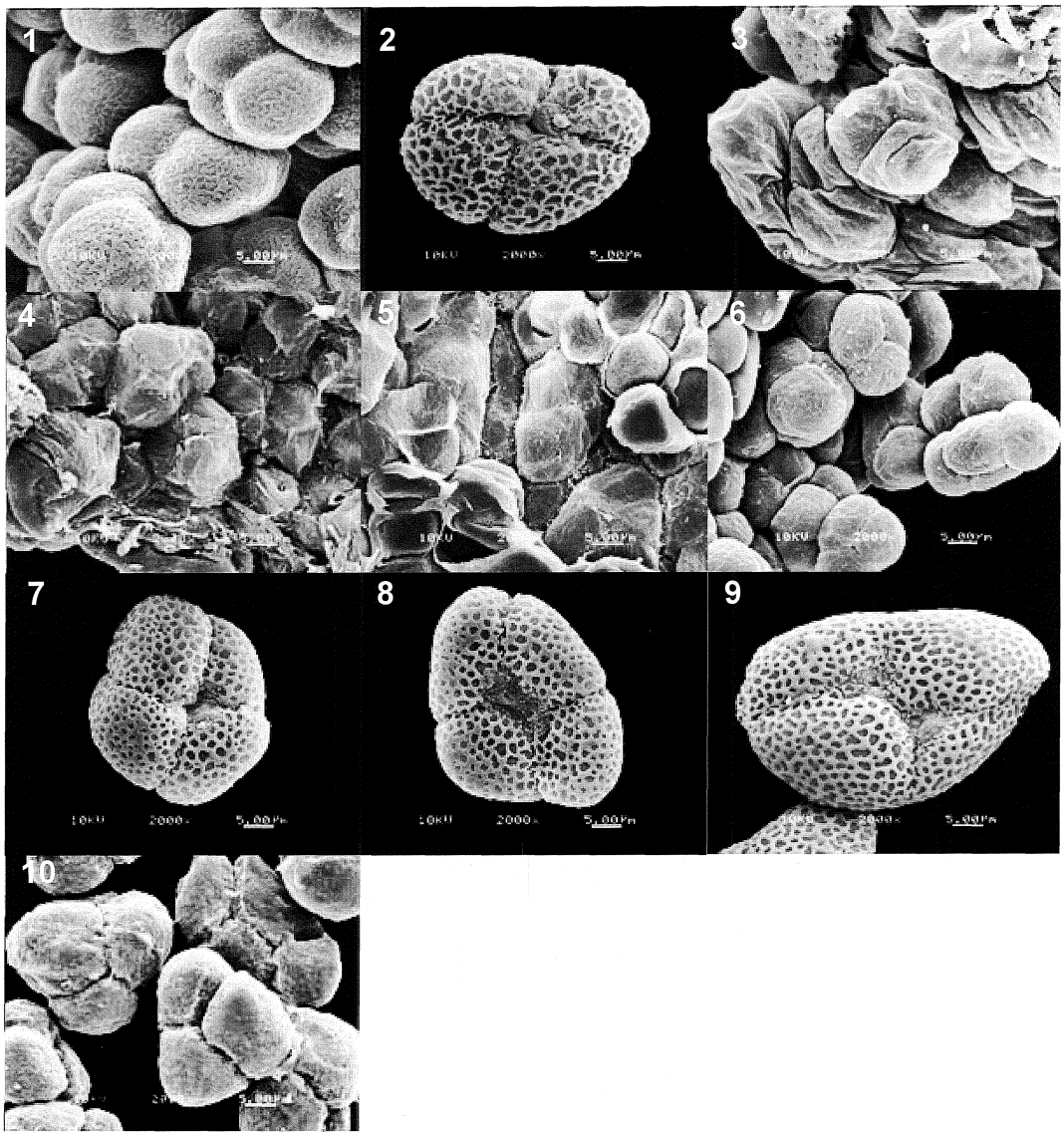

FIGURE 3: 1. Orchids of Soconusco, southeastern Mexico (Tribes Cranichideae, Sobralieae, Ponerinae): Photographs of images taken by a scanning electron microscope of the tetrads towards the interior of the pollinia, after processing and dry-fracture. Images augmented x 2000 and taken under conditions of high vacuum at 10–15 kV. 1) *Coelia macrostachya,* 2) *Aulosepalum hemichreum,* 3) *Elleanthus cynarocephalus,* 4) *Isochilus carnosiflorus,* 5) *Isochilus* aff. *major,* 6) *Nemaconia striata,* 7) *Sarcoglottis* sp. 1, 8) *Sarcoglottis* sp. 2, 9) *Sarcoglottis sceptrodes,* 10) *Sobralia macrantha.*

within these taxonomic groups, trends are clear for each subfamily and tribe. The pollinia of the tribe Pleurothallidinae lack accessory structures (caudicle or stipe). The genera *Stelis* and *Trichosalpinx* have an accumulation of sticky material with a few pollen grains stuck to it at one extreme, and the pollinia of *Platystele, Pleurothallis* and *Specklinia* are free and juxtaposed at one side. The pollinia of the Oncidiinae have a stipe which is generally long and wide and a viscidium, with the exception of *Lockhartia verrulos, Cuitlauzina convallarioides* and *Trichocentrum oerstedii,* for which it is difficult to determine whether the accessory structure is a very short stipe or only a viscidium. The results for all the species are presented in TABLE 2:3.

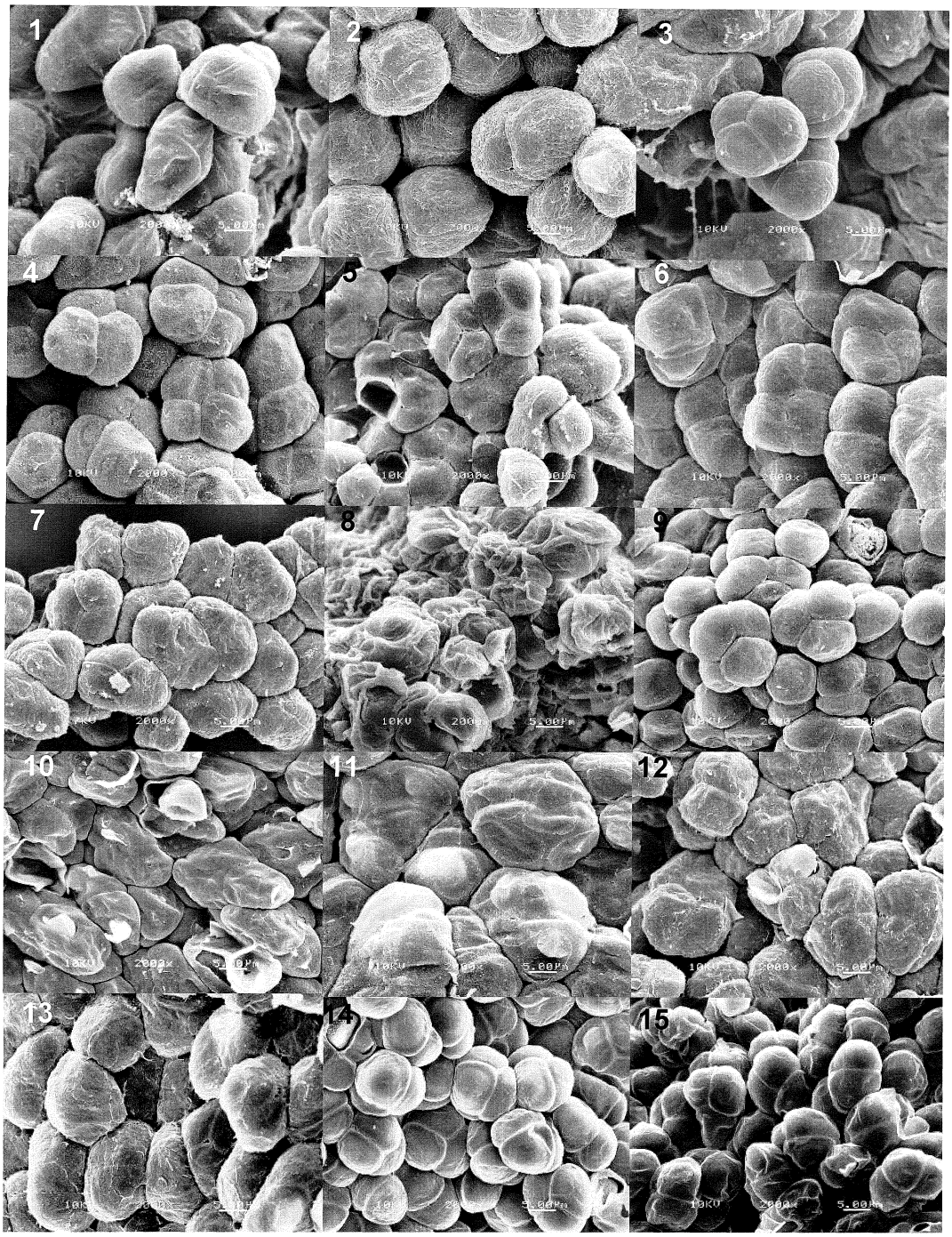

FIGURE 3: 2. Orchids of Soconusco, southeastern Mexico from the subtribe Laeliinae (Tribe Epidendreae): Photographs of images taken by a scanning electron microscope of the tetrads towards the interior of the pollinia, after processing and dry-fracture. Images augmented x 2000 and taken under conditions of high vacuum at 10–15 kV. 1) *Barkeria obovata,* 2) *Barkeria skinneri,* 3) *Brassavola nodosa,* 4) *Caularthron bilamellatum,* 5) *Encyclia adenocarpa,* 6) *Encyclia parviflora,* 7) *Encyclia cordigera,* 8) *Encyclia selligera,* 9) *Encyclia bractescens,* 10) *Epidendrum ciliare,* 11) *Epidendrum lacertinum,* 12) *Epidendrum melistagum,* 13) *Epidendrum stamfordianum,* 14) *Guarianthe aurantiaca,* 15) *Guarianthe skinneri,* 16) *Jacquiniella cobanensis,* 17) *Laelia*

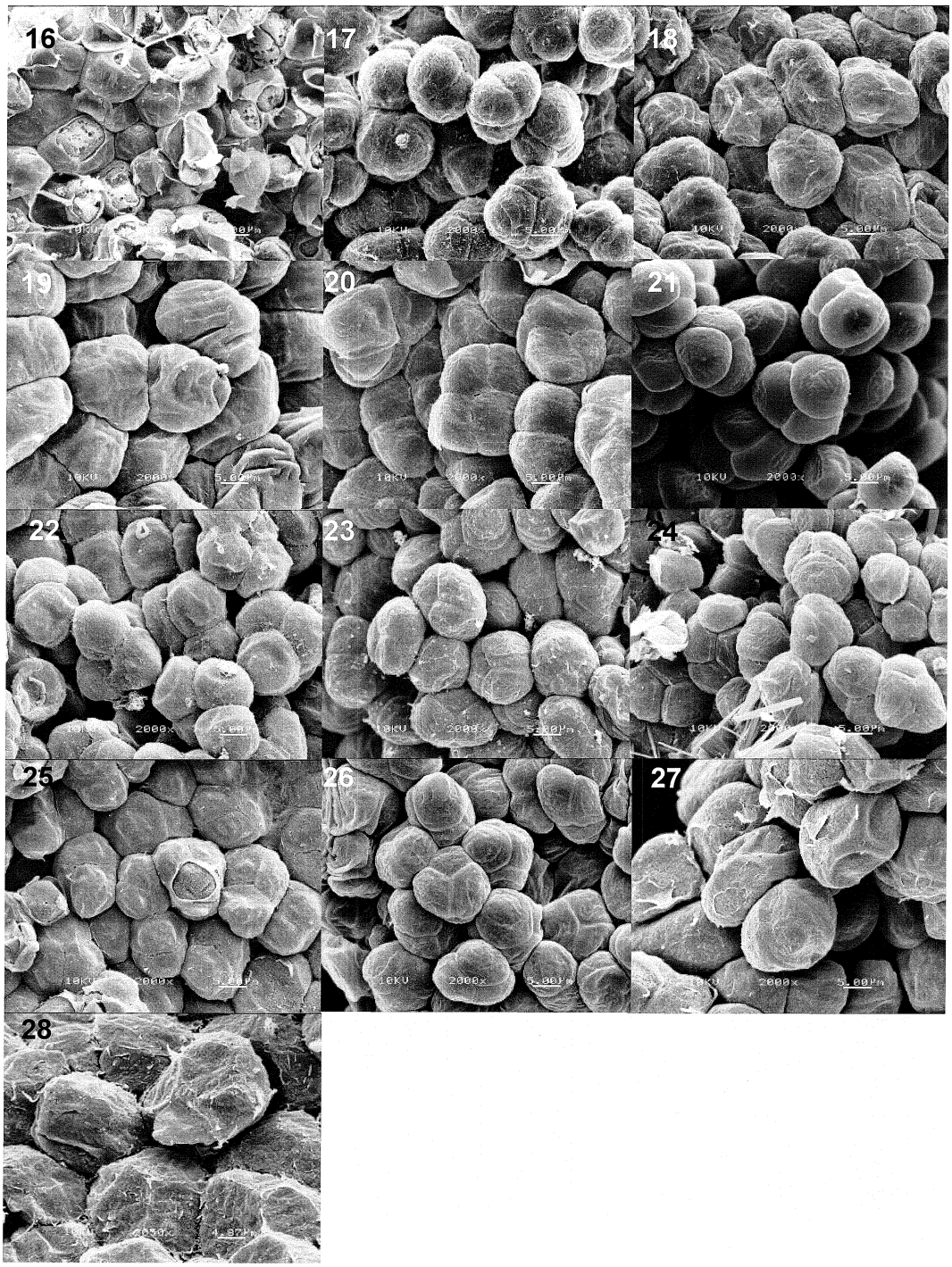

FIGURE 3: 2. (Continued) *rubescens,* 18) *Meiracyllium trinasutum,* 19) *Nidema boothii,* 20) *Prosthechea baculus,* 21) *Prosthechea chacaoensis,* 22) *Prosthechea chondylobulbon,* 23) *Prosthechea cochleata,* 24) *Prosthechea livida,* 25) *Prosthechea ochracea,* 26) *Prosthechea radiata,* 27) *Scaphyglottis crurigera,* 28) *Scaphyglottis* sp.

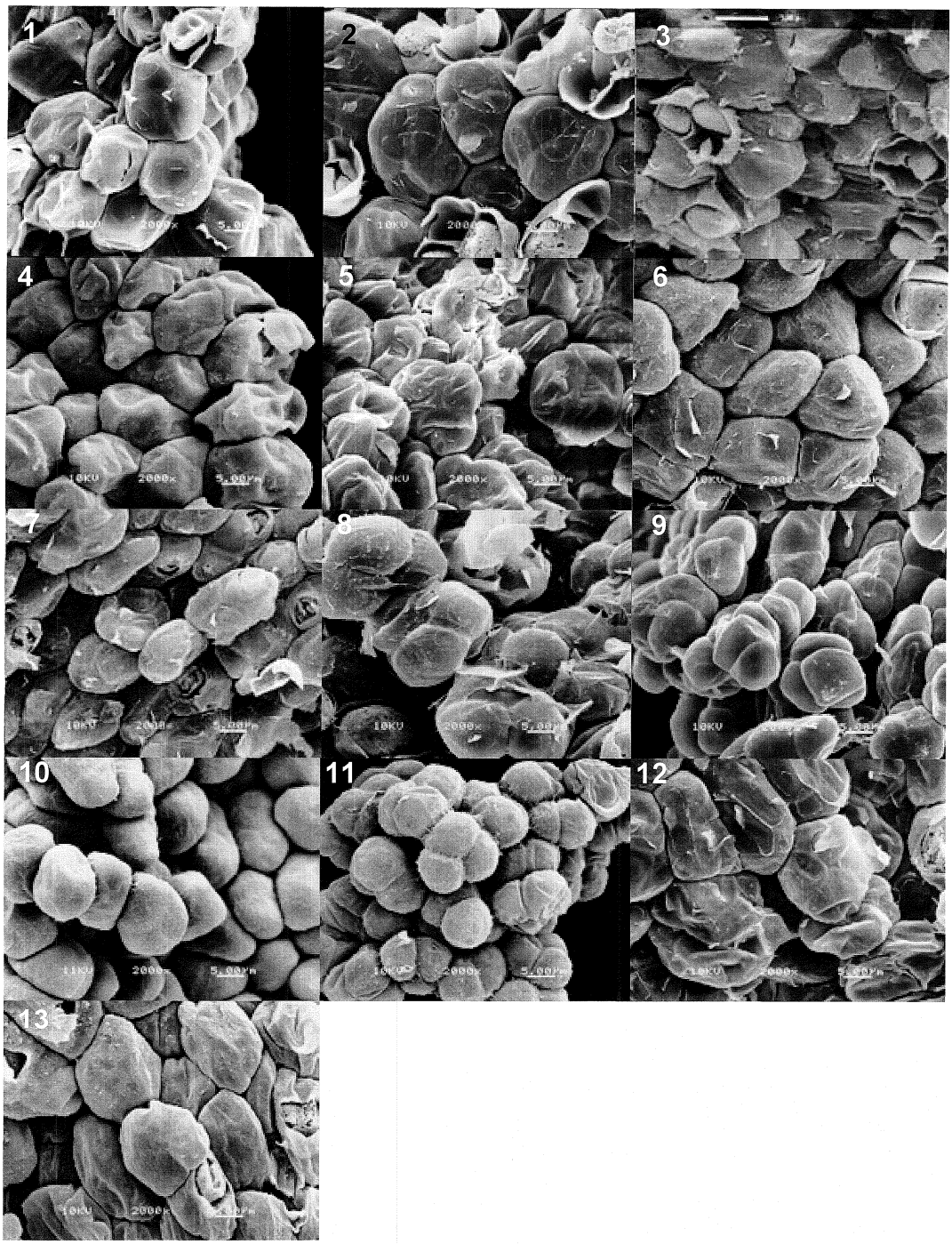

FIGURE 3: 3. Orchids of Soconusco, southeastern Mexico from the Tribe Pleurothallidinae (Subfamily Epidendreae) and Tribe Oncidiinae (Subfamily Cymbidiae): Photographs of images taken by a scanning electron microscope of the tetrads towards the interior of the pollinia, after processing and dry-fracture. Images augmented x 2000 and taken under conditions of high vacuum at 10–15 kV. 1) *Brassia verrucosa,* 2) *Erycina crista-galli,* 3) *Leochilus* aff. *labiatus,* 4) *Lockhartia verrucosa,* 5) *Oncidium laeve,* 6) *Oncidium ornithorrhynchum,* 7) *Oncidium sphacelatum,* 8) *Ornithocephalus tripterus,* 9) *Cuitlauzina convallarioides,*10) *Stelis quadrifida,* 11) *Trichocentrum ascendens,* 12) *Trichocentrum microchilum,* 13) *Trichopilia tortilis.*

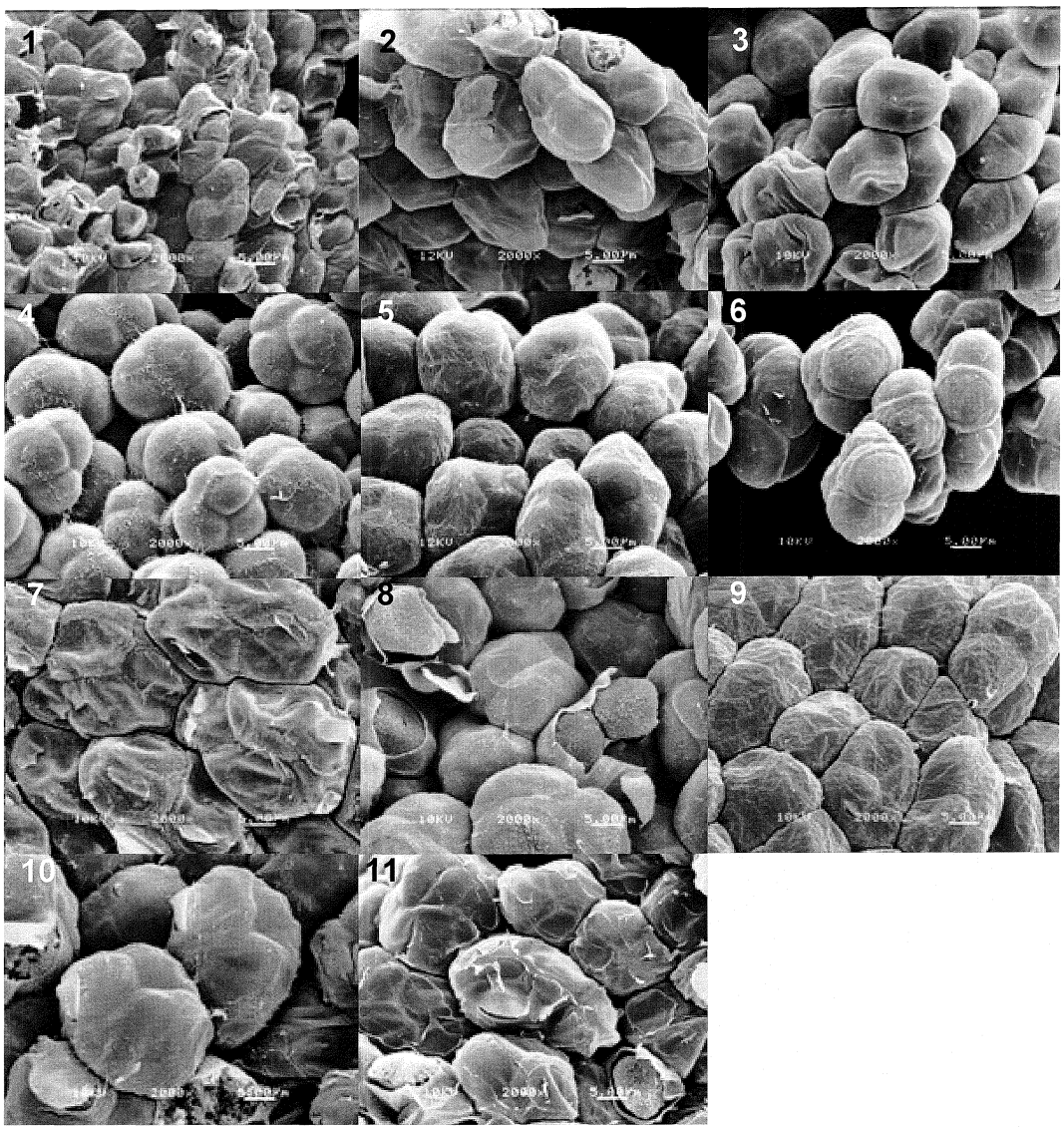

FIGURE 3: 4. Orchids of Soconusco, southeastern Mexico from the Tribes: Catesinae, Eulophiinae, Maxillariinae, Stanhopeinae, Zygopetilinae (Subfamily Cymbidiae) and Tribes: Polystachyinae, Angraecinae (Subfamily Vandeae): Photographs of images taken by a scanning electron microscope of the tetrads towards the interior of the pollinia, after processing and dry-fracture. Images augmented x 2000 and taken under conditions of high vacuum at 10–15 kV. 1) *Kefersteinia tinschertiana,* 2) *Maxillaria parviflora,* 3) *Maxillaria densa,* 4) *Maxillaria friedrichsthalii,* 5) *Maxillaria hagsateriana,* 6) *Maxillaria variabilis,* 7) *Maxillaria* aff. *elatior,* 8) *Mormodes lineata,* 9) *Mormolyca ringens,* 10) *Oeceoclades maculata,* 11) *Polystachya foliosa.*

Subtribe Pleurothallidinae

The pollinia of the Pleurothallidinae are the smallest (TABLE 1:3) of all the orchid species found in Soconusco and are variable in shape, obovate for *Stelis,* spherical for *Platystele ovatilabia,* and lenticular for *Pleurothallis* and *Specklinia.* The pollinia of *P. ovatilabia, Pleurothallis* and *Specklinia* (FIGURE 1:3, Nos. 15–20) have neither accessory structures nor a visible accumulation of sticky material (viscidium) that would facilitate adherence to the pollinator; it is possible, however, that the entire surface of the pollinia is sticky. The pollinia of *Stelis quadrifida* and *Trichosalpinx blaisdellii* (FIGURE 1:3, Nos. 21, 22, 28) have an accumulation of viscin

and individual pollen grains stuck to it at one extreme, which could be interpreted as an undifferentiated caudicle. Stenzel (2000) describes the pollinia of the subtribe Pleurothallidinae as having undifferentiated caudicles, and similar sizes are reported for the pollinia of *Stelis* (250–400 μm), *Trichosalpinx* (200–300 μm) and *Platystele* (70–120 μm).

The texture of the pollinia of this group are hard compact 2, which can be observed at the cut surface of the fractured pollinia, wherein the majority of the pollen grains are split open, with the exception of *Stelis quadrifida* (FIGURE 2:3, Nos. 14, 21, 23), which maintains intact pollen grains when the pollinia are fractured and are classified as soft compact (FIGURE 2:3, Nos. 16–19, 21, 27). It was not possible to fracture the pollinia of *P. ovatilabia* due to their very small size. It is not possible to determine the arrangement of the tetrads of *Stelis quadrifida* which are enveloped in a common covering (calymmate) (FIGURE 3:3, No. 10).

In our study, the ornamentation of the exine layer is distinct for every species within this tribe, and even for species of the same genus. *P. ovatilabia* (FIGURE 4:3, No. 15) has laevigate ornamentation of the exterior surface and pits of between 0.4 and 1μm (foveolate) on the internal surface. The two species of *Pleurothallis* (FIGURE 4:3, Nos. 16, 17) can easily be distinguished: one is foveolate and the other laevigate on both surfaces. The three species of *Specklinia* (FIGURE 4:3, Nos. 18, 19, 20) are also distinguishable: although they coincide in being without ornamentation on the interior surface, two are laevigate *S. lateritia and S. tribuloides* Fig. 4.3, Nos. 18, 20 and the other hamulate *S. marginata* Fig. 4.3 No. 19 on the exterior surface. Although the two species of *Stelis* (FIGURE 4:3, Nos. 21, 22) are laevigate on the external surface, they can be distinguished because the internal surface of the exine layer of *S. quadrifida* is scabrate and fine, almost laevigate; whereas that of *Stelis* sp. is gemmate. *Trichosalpinx blaisdellii* has gemmate ornamentation on the exterior wall (FIGURE 4:3, Nos. 21, 22, 28).

Stenzel (2000) reported that the ornamentation of the exine layer of *Platystele* was psilate (laevigate), disintegrating towards the edge; however, in our sample of *P. ovatilabia,* the ornamentation is clearly foveolate. For *Pleurothallis,* Stenzel reported an undifferentiated, punctate ornamentation, similar to one of the species in our study, but different from the second species which has a thick wall interrupted by hollows of varying sizes which run the length of the walls and join together to form larger gaps and constrictions, like gems of less than 1μm. Similarly, Zavada (1990) described the external walls of *P. janetiae* as rugulate. Stenzel (2000) gave similar descriptions for *Stelis* (ornamentation predominantly psilate to punctate) and *Trichosalpinx* (gemmate) similar to the *Stelis* of our study.

The characteristics of the pollinia that stand out for this subtribe are the 2 pollinia, the undifferentiated caudicle, and the compact hard 2 texture.

Subtribe Oncidiinae

The pollinia of the species of this subtribe are globose, due to the folding of the pollen mass, similar to many vandoid orchids, as reported by Freudenstein et al. (2002). The almost spherical shape present in *Ionopsis* and some *Leochilus,* becomes more obovate in the majority of *Oncidium* and *Trichocentrum,* elliptical in *Ornithocephalus* and *Lockhartia* and some *Leochilus,* and pear-shaped in *Brassia* and *Osmoglossum.*

The majority of the pollinia (FIGURE 1:3, Nos. 1–7, 9–13, 22–24, 26) possess a clearly visible stipe, as described by Dressler (1993) for the advanced Epidendroideae. The size of the stipe varies from 0.81 to 1.97 with the exception of *Oncidium ornithorrynchum* and *Osmoglossum pulchellum,* with stipes of 3.01 and 0.4 mm long, respectively (see FIGURE 1:3, Nos. 11, 14). The width of the stipes varies from 0.23 to 0.60 mm for the majority, with the exception of *Ionopsis satyrioides* with narrow stipe of 0.11 mm in width. At the other extreme to the pollinia there is a triangular or lingulate viscidium. For *Lockhartia oerstedii, O. pulchellum* and *Trichocentrum oerstedii* (see FIGURE 1:3, Nos. 8, 14, 25) it is impossible to determine whether or not there is a short stipe underneath the viscidium.

The range of sizes for this subtribe is limited: all fall within the range 0.43–1.54 μm in length and 0.26–0.94 μm in width, with the smallest being *I. satyrioides, Leochilus* and *Ornithocephalus tripterus* (0.33 × 0.30 and 0.24 × 0.18 μm), and the largest *Trichopilia tortilis* (0.64 × 0.72 mm). There is little information in the literature about the morphology of the pollinia of these species, but it is possible to compare the form and number of pollinia that we mention here, with the report by Roubik (2003) in the web page of the Smithsonian Tropical Research Institute, where some of the same species and genera are presented.

The texture of the majority of the pollinia in this group is hard compact, to such an extent that in some species the walls of the pollen grain break open when the pollinia are fractured, corresponding to the classification hard compact 2, as for the majority of *Leochilus, L. oerstedii* and *Notylia barkeri* (FIGURE 2:3, Nos. 3, 5–7, 8, 9). In other species, the majority of the grains re-

main entire, but are tightly joined, corresponding to the classification of hard compact 1, as for *Brassia verrucosa, Erycina crista-galli* and *Oncidium* (FIGURE 2:3, Nos. 1, 2, 10–12). To the contrary, *C. convallarioides* and *Trichocentrum ascendens* have pollinia with a soft compact texture, in which the interior tetrads separate easily (FIGURE 2:3, Nos. 14, 22).

The tetrads can be distinguished only in some species with hard and soft texture (FIGURE 3:3) as the majority are wrapped in a common covering (calymmate). It was possible to distinguish the arrangement of the tetrads only in *Oncidium laeve, O. tripterus, C. convallarioides,* and *T. ascendens,* which was either rhomboid or tetrahedral, or both (see FIGURE 3:3, Nos. 5, 8, 9, 11).

The ornamentation of the exine layer of the majority of species is laevigate on the outer walls and scabrate on the internal walls (*Brassia, Erycina, Oncidium, Trichocentrum*) (FIGURE 4:3, Nos. 1, 2, 10–12, 22–25); in the case of *Leochilus,* the exterior walls have perforations of different sizes and density (FIGURE 4:3, Nos. 3–6); in *T. tortilis* the external wall is thick, with elongated, or fossulate, perforations (FIGURE 4:3, No. 26).

From the morphological analysis of the pollinaria and pollinia, we suggest that the purple-leaved *Leochilus* aff. *labiatus* may be a separate, as yet unidentified species.

All the specimens from this tribe have 2 pollinia, with the exception of *O. tripterus,* which has 4. All have a stipe and a compact hard type 1 or 2 texture.

Section 4

Subfamily Cymbidiae: Tribe Catesinae (*Catasetum, Cycnoches, Mormodes*), Tribe Eulophiinae (*Oeceoclades*), Tribe Maxillariinae (*Maxillaria, Mormolyca, Trigonidium*), Tribe Stanhopeinae (*Gongora, Stanhopea*). Tribe Zygopetilinae (*Kefersteinia*). Subfamily Vandeae: Tribe Polystachyinae (*Polystachya*), Tribe Angraecinae (*Campylocentrum*).

All the species studied in the subfamilies Cymbidiae and Vandeae have two or four pollinia, with a wide variety of forms and sizes of both pollinia and accessory structures. Forms range from almost spherical (*Campylocentrum micranthum,* both species of *Cycnoches* and *Polystachya foliosa*) to elliptical elongated and flattened *Gongora galeata* and *Stanhopea saccata*). The accessory structures are varied. Some pollinia have undifferentiated or imperceptible accessory structures (*Maxillaria hagsateriana*). The stipe may be thin, like a cord (*Maxillaria densa*); like a long, wide belt (*Catasetum integerrimum,* both species of *Cycnoches, Maxillaria friedrichsthallii, Maxillaria lineata,* among others); or a short wide belt (*Kefersteinia tinschertiana*). In other cases, besides the stipe there is a viscidium in the shape of an arch (*Maxillaria* aff. *eliator, Maxillaria ringens, Mormolyca ringens* among others), a disk (*P. foliosa*), or an arrow (*Oeceoclades maculata*). The complete set of results for this section is presented in TABLE 2:3.

Tribe Catesinae

The species of this tribe share the characteristic of globose-shaped pollinia due to the folding of the pollen mass, and the stipe resembles a wide belt with a disk-shaped viscidium at one extreme. The pollinia are among the largest of the 91 species studied, with *Catasetum integerrinum* the largest of all (4.98 × 3.05 mm) (FIGURE 1:4, Nos. 2–4, 14). The pollinia of the two species of *Cycnoches* are very similar, although one species is almost twice the size of the other.

C. integerrinum, Cycnoches ergotonianum and *C. ventricosum* have pollinia with a hard compact 2 texture, and the pollen grains split open when the tetrads are fractured (FIGURE 2:4, Nos. 2–4); while *Mormodes lineata* (FIGURE 2: 4, No. 14) has pollinia classified as hard compact 1, and the pollen grains do not split when the tetrads are fractured, making it possible to observe that the tetrads have a rhomboid arrangement (FIGURE 3:4, No. 8).

The ornamentation of the exine layer of the external surface of the surface tetrads is similar for all the species studied, resembling granular depositions, although the size and the smoothness of the internal walls are variable. These differences permit us to distinguish between *C. ventricosum* and *C. ergotonianum* (FIGURE 4:4, No. 3): the former has thicker granules, like warts, on both the internal and external walls, whereas *C. ergotonianum*) (FIGURE 4:4, No. 4) has smaller and more uniform granules with a smoother internal surface.

The species studied from the tribe Catesinae have 2 pollinia, a long and wide stipe, hard texture, and similar exine ornamentation.

Tribe Maxillariinae

The pollinaria of the species of *Maxillaria* studied have a great variety of forms and sizes of pollinia and accessory structures. All have four pollinia, and various are asymmetrical in size (two big, two small). The smallest pollinia belong to *M. parviflora, M. densa* and *M. hagsateriana,* which all have obovate, symmetrical pollinia less than 0.5 mm long and not more than 0.4 mm wide (FIGURE 1:4, Nos. 7, 8, 11). The largest pollinia belong to *M.* aff. *eliator* (FIGURE 1:4, No. 9), which measure

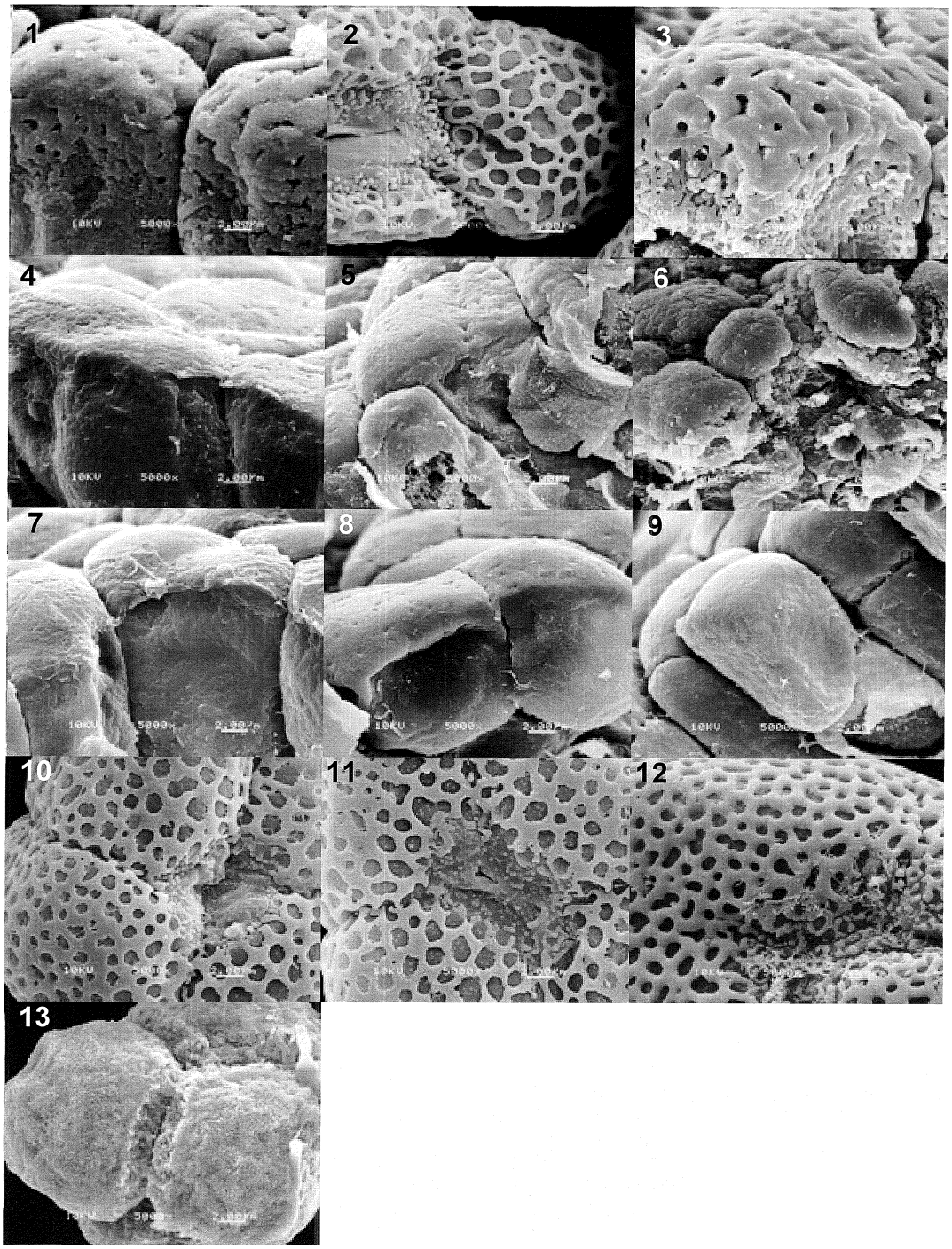

FIGURE 4: 1. Orchids of Soconusco, southeastern Mexico (Tribes Cranichideae, Sobralieae, Ponerinae): Photographs of images taken by a scanning electron microscope of the exine layer of the interior and exterior walls of the surface tetrads of pollinia. Images augmented x 5000 and taken under conditions of high vacuum at 10–15 kV. 1) *Coelia macrostachya,* 2) *Aulosepalum hemichreum,* 3) *Elleanthus cynarocephalus,* 4) *Isochilus carnosiflorus,* 5) *Isochilus* aff. *latibracteatus,* 6) *Isochilus* aff. *linearis,* 7) *Isochilus* aff. *major,* 8) *Isochilus* sp., 9) *Ponera striata,* 10) *Sarcoglottis* sp. 1, 11) *Sarcoglottis* sp. 2, 12) *Sarcoglottis sceptrodes,* 13) *Sobralia macrantha.*

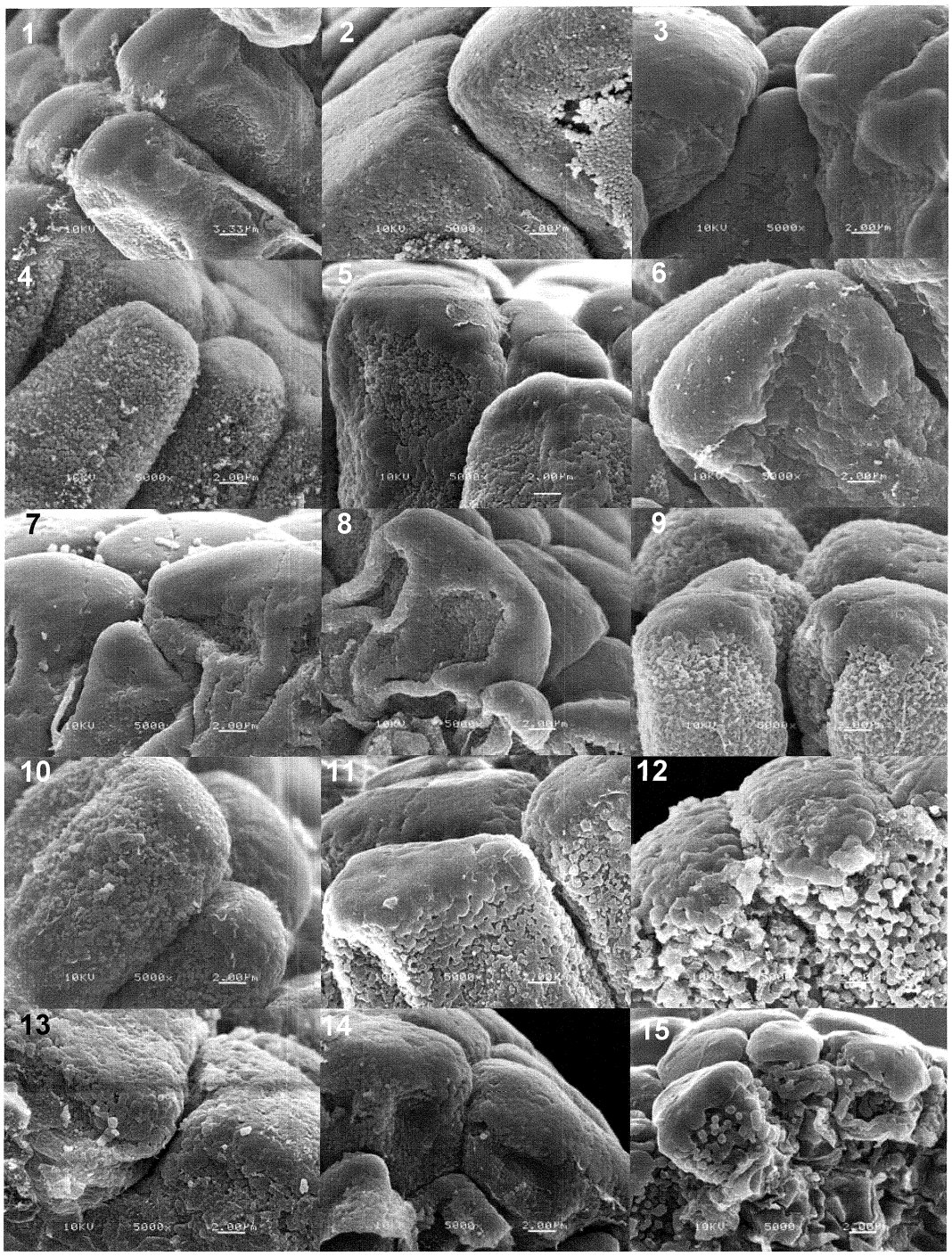

FIGURE 4: 2. Orchids of Soconusco, southeastern Mexico from the subtribe Laeliinae (Tribe Epidendreae): Photographs of images taken by a scanning electron microscope of the exine layer of the interior and exterior walls of the surface tetrads of pollinia. Images augmented x 5000 and taken under conditions of high vacuum at 10–15 kV. 1) *Barkeria obovata,* 2) *Barkeria skinneri,* 3) *Brassavola nodosa,* 4) *Caularthron bilamellatum,* 5) *Encyclia adenocarpa,* 6) *Encyclia parviflora,* 7) *Encyclia cordigera,* 8) *Encyclia selligera,* 9) *Encyclia bractescens,* 10) *Epidendrum ciliare,* 11) *Epidendrum lacertinum,* 12) *Epidendrum melistagum,* 13) *Epidendrum polyanthum,* 14) *Epidendrum stamfordianum,* 15) *Epidendrum ramosum,* 16) *Guarianthe aurantiaca,* 17) *Guarianthe skinneri,* 18) *Jacquiniella*

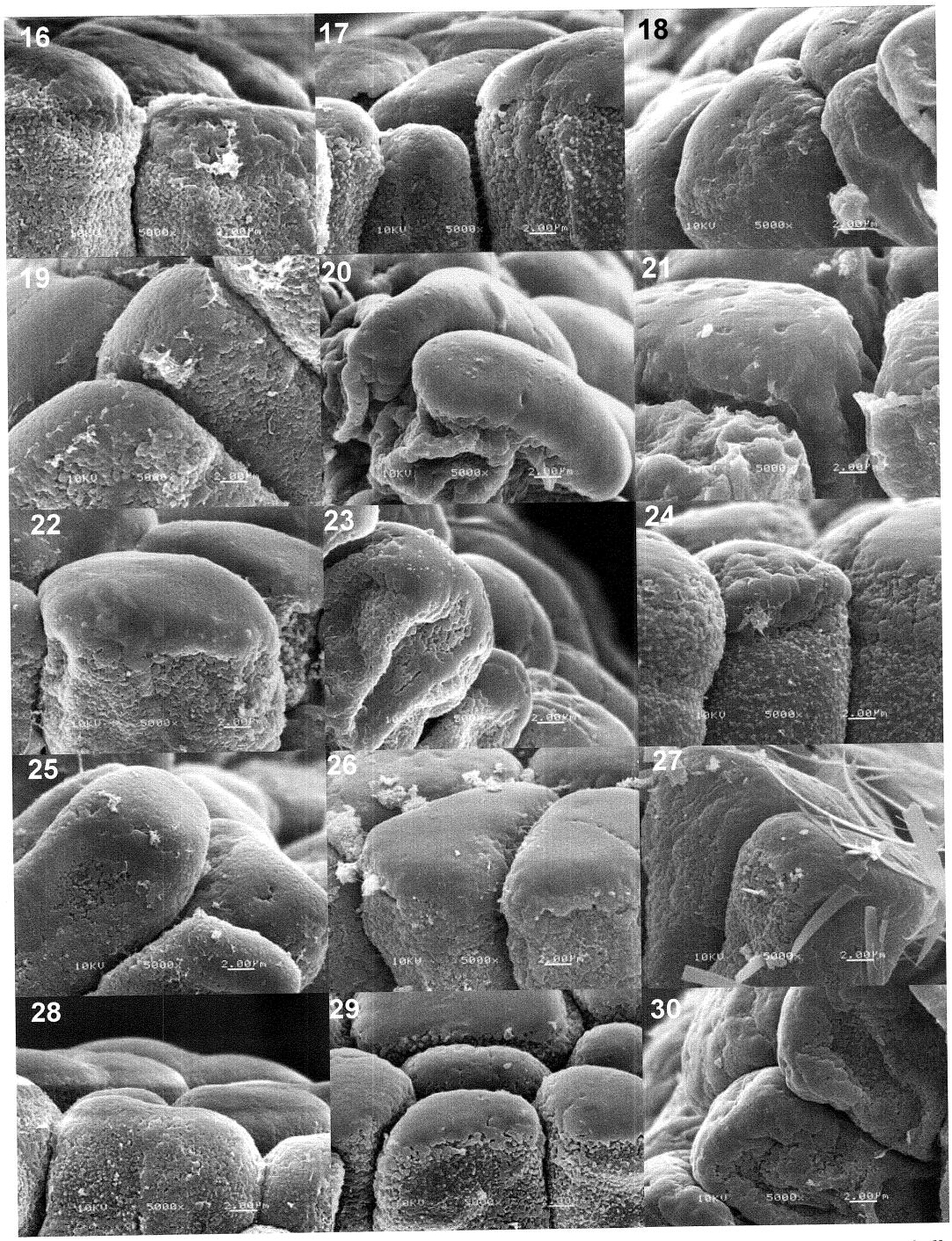

FIGURE 4: 2. (Continued) *cobanensis,* 19) *Laelia rubescens,* 20) *Meiracyllium trinasutum,* 21) *Nageliella purpurea,* 22) *Nidema boothii,* 23) *Prosthechea baculus,* 24) *Prosthechea chacaoensis,* 25) *Prosthechea chondylobulbon,* 26) *Prosthechea cochleata,* 27) *Prosthechea livida,* 28) *Prosthechea ochracea,* 29) *Prosthechea radiata,* 30) *Scaphyglottis crurigera,* 31) *Scaphyglottis* sp.

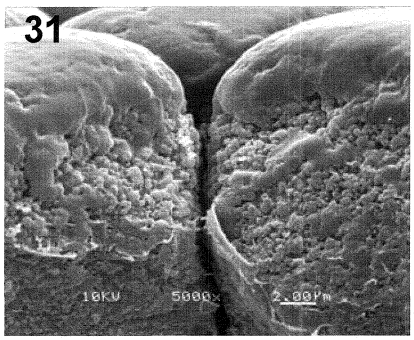

FIGURE 4: 2. Continued.

1.89 × 1.22 mm, and are obovate in form with one side flattened. *Mormolyca ringens* (FIGURE 1: 4, No. 15) has four obovate asymmetrical pollinia, with one straight side, measuring 0.92 and 0.72 mm in length (large and small, respectively); and *Trigonidium ergotonianum* (see FIGURE 1:4, No. 19) has two symmetrical pollinia with a narrow elliptical shape and one flat face, measuring 0.89 × 0.36 mm.

Singer and Koehler (2004), in their study of Brazilian Maxillariinae, reported that all the species studied had four pollinia which are presented in two pairs, each pair generally composed of a larger and a smaller one. In our study, three species of *Maxillaria* (*M. parviflora, M. densa* and *M. hagsateriana*) have four pollinia of the same size, although in the photograph (FIGURE 1: 4, No. 7), *M. parviflora* appears to have one pollinia larger than the rest, which was probably an artifact of the orientation or handling of the sample; some samples were noticeably more sensitive and more easily deformed when submitted to low vacuum than others.

The accessory structures of the maxillarias studied are varied: *M. parviflora* has a short and wide stipe, *M. densa* has a short but thin stipe resembling a cord, and *M. friedrichsthallii* has a long and wide stipe. *M.* aff *eliator, M. ringens* and *M. variabilis* do not have stipes; in their place, the pollinia rest upon arch-shaped viscidia, with variable widths and apertures. The pollinia of *M. hagsateriana* have no visible accessory structures. It is possible that the viscin simply accumulates toward one extreme of the pollinia, or that there had been a thin and delicate cord, similar to that of *M. densa,* to which it bears most resemblance, and that the pollinia became detached during collection and transport. Unfortunately, there was insufficient biological material to repeat the analysis. Singer and Koehler (2004) report four kinds of accessory structures that were also present in our samples: the arch-shaped viscidium type 1 as in *M. ringens*; the thin viscidium type 2 as for *M.* aff. *eliator*; the rigid viscidium type 3 as for *M. variabilis;* and the long and wide stipe type 4 as for *M. friedrichsthallii.* However, in our study we found a further type of accessory structure, which was the thin, cord-like stipe of *M. densa.*

Mormolyca ringens and *Trigonidium ergotonianum* both have an arch-shaped viscidium, and it is difficult to distinguish if there is a tergite stipe between the pollinia and the viscidium as described by Singer and Koehler (2004) for these genera.

The texture of the pollinia of *Maxillaria* is soft compact. Some of the tetrads are enveloped by a common covering (calymmate), as seen for *M. parviflora* and *M. densa* (FIGURE 2:4, Nos. 7, 8 and FIGURE 3:4, Nos. 2, 3), whereas others can be seen to have a tetrahedral arrangement, as for *M. variabilis* (FIGURE 2:4, No. 13 and FIGURE 3: 4, No. 6). The pollinia of *M. ringens* (FIGURE 2: 4, No. 12) collapsed during processing, and it was not possible to interpret either the arrangement of the tetrads or the texture, although indications are that the texture is soft, as for the other species of *Maxillaria* studied. The pollinia of *Mormolyca ringens* also have a soft texture with calymmate tetrads, but that of *Trigonidium ergotonianum* have a hard compact texture.

The ornamentation of the exine layer of all the species studied in this tribe is basically laevigate on the external surface of the tetrads and with the ornamentation slightly more defined on the internal surface, with faint granulations (FIGURE 4:4, Nos. 7–13, 15, 19). However, this characteristic is not very useful to distinguish between species, although it may be useful at higher taxonomic levels.

Tribes Eulophiinae, Stanhopeinae, Zygopetilinae

The pollinaria of all the species in these tribes carry two pollinia (FIGURE 1:4, Nos. 5, 16, 18). *Gongora galeata* and *Stanhopea saccata* have relatively long stipes (1.79 and 3.02 mm, respectively), and *Oeceoclades maculata* (FIGURE 1:4, No. 16) has a short stipe that fuses with a large viscidium in the form of an arrow. The exception is *Kefersteinia tinschertiana* (FIGURE 1:4, No. 6) with four asymmetrical pollinia and a relatively short stipe, measuring 1.02 mm. The form of the pollinia of the Stanhopeinae and *K. tinschertiana* is elongated, that of *O. maculata* is wide and trulloid, with one flat side. *S. saccata* is one of the species with the largest pollinia (3.02 × 0.90 mm).

The texture of the pollinia of these species ranges from soft compact as for *O. maculata* (FIGURE 2:4, No. 16) with calymmate tetrads, to the other extreme of hard compact 2 in which,

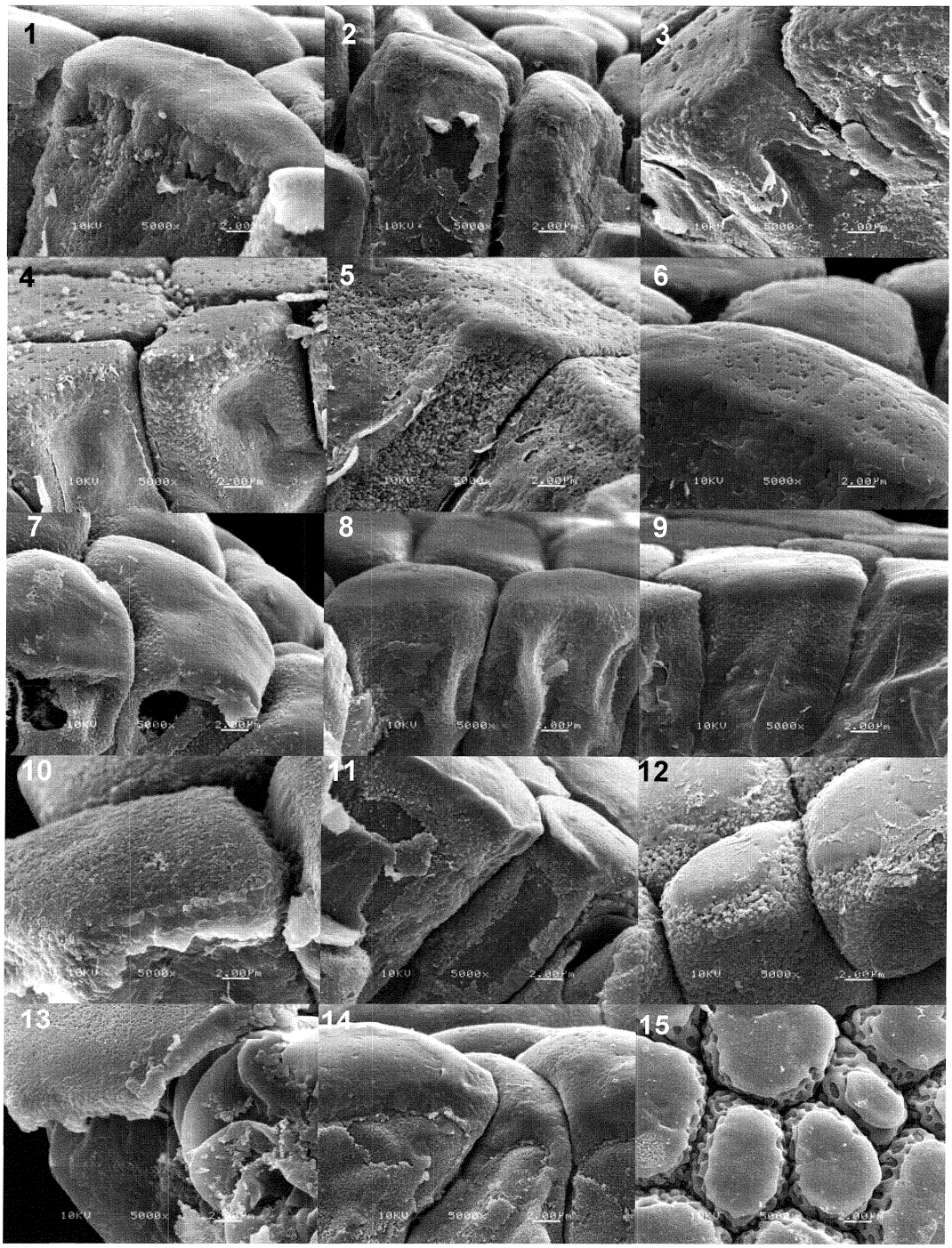

FIGURE 4: 3. Orchids of Soconusco, southeastern Mexico from the Tribe Pleurothallidinae (Subfamily Epidendreae) and Tribe Oncidiinae (Subfamily Cymbidiae): Photographs of images taken by a scanning electron microscope of the exine layer of the interior and exterior walls of the surface tetrads of pollinia. Images augmented x 5000 and taken under conditions of high vacuum at 10–15 kV. 1) *Brassia verrucosa,* 2) *Erycina crista-galli,* 3) *Leochilus labiatus,* 4) *Leochilus* aff. *labiatus,* 5) *Leochilus scriptus,* 6) *Leochilus oncidioides,* 7) *Ionopsis satyrioides,* 8) *Lockhartia verrucosa,* 9) *Notylia barkeri,* 10) *Oncidium laeve,* 11) *Oncidium ornithorrhynchum,* 12) *Oncidium sphacelatum,* 13) *Ornithocephalus tripterus,* 14) *Cuitlauzina convallarioides,*

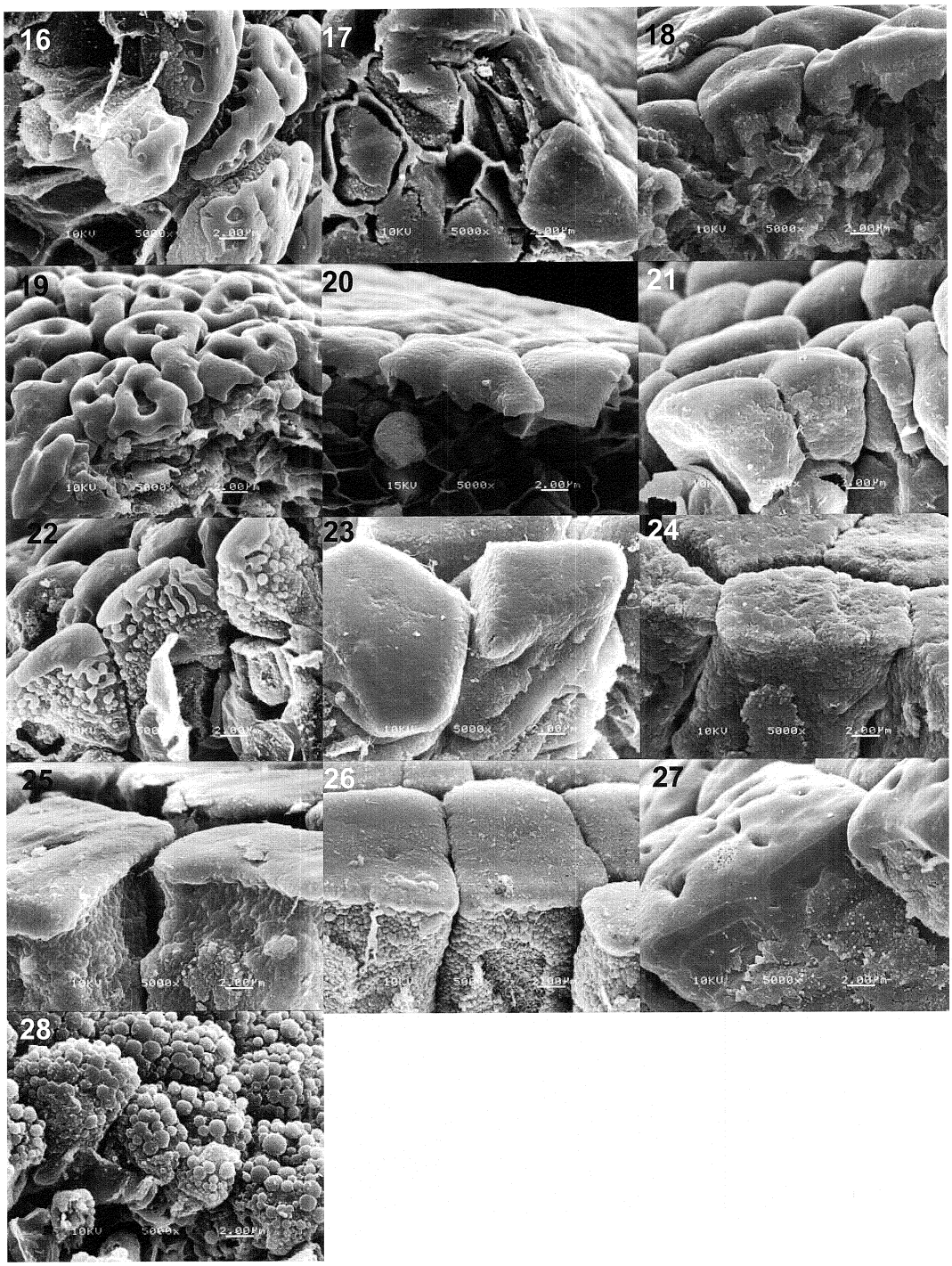

FIGURE 4: 3. (Continued) 15) *Platystele ovatilabia,* 16) *Pleurothallis* sp. 1, 17) *Pleurothallis* sp. 2, 18) *Specklinia lateritia,* 19) *Specklinia marginata,* 20) *Specklinia tribuloides,* 21) *Stelis quadrifida,* 22) *Stelis* sp., 23) *Trichocentrum ascendens,* 24) *Trichocentrum candidum,* 25) *Trichocentrum microchilum,* 26) *Trichocentrum oerstedii,* 27) *Trichopilia tortilis,* 28) *Trichosalpinx blaisdellii.*

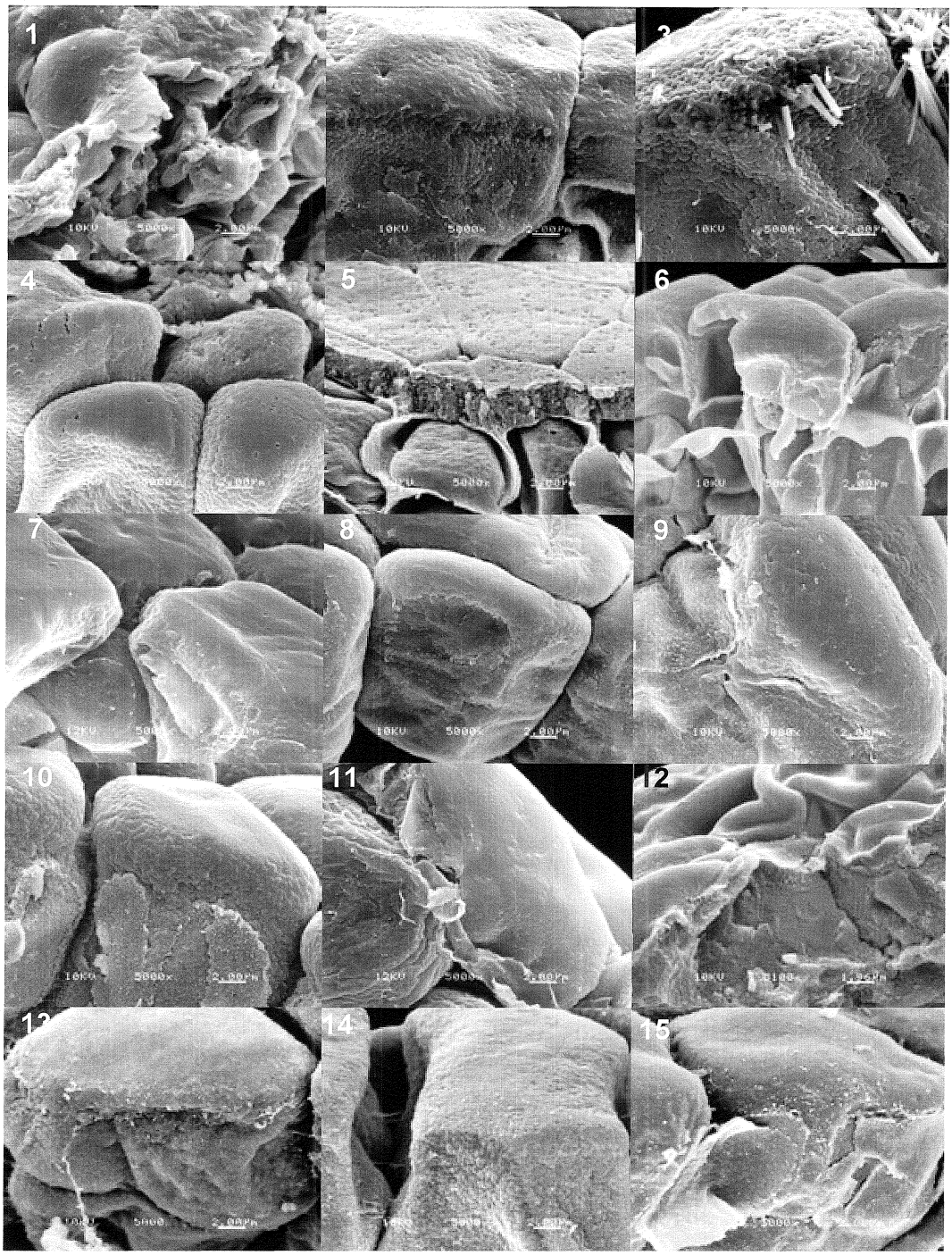

FIGURE 4: 4. Orchids of Soconusco, southeastern Mexico from the Tribes: Catesinae, Eulophiinae, Maxillarinae, Stanhopeinae, Zygopetilinae (Subfamily Cymbidiae) and Tribes: Polystachyinae, Angraecinae (Subfamily Vandeae): Photographs of images taken by a scanning electron microscope of the exine layer of the interior and exterior walls of the surface tetrads of pollinia. Images augmented x 5000 and taken under conditions of high vacuum at 10–15 kV. 1) *Campylocentrum micranthrum,* 2) *Catasetum integerrimum,* 3) *Cycnoches egertonianum,* 4) *Cycnoches ventricosum,* 5) *Gongora galeata,* 6) *Kefersteinia tinschertiana,* 7) *Maxillaria par-*

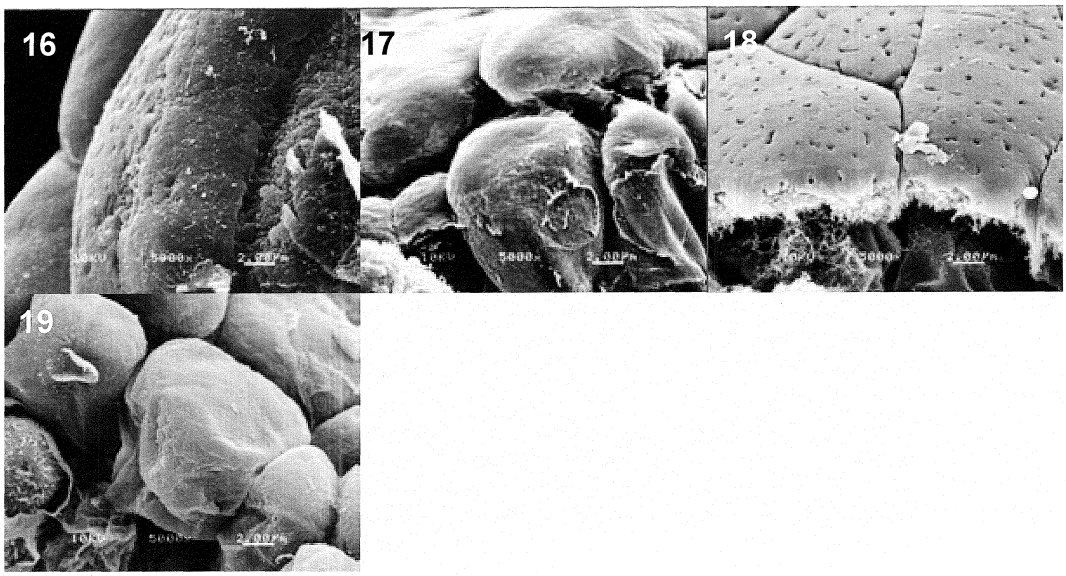

FIGURE 4: 4. (Continued) *viflora,* 8) *Maxillaria densa,* 9) *Maxillaria* aff. *elatior,* 10) *Maxillaria friedrichsthalii,* 11) *Maxillaria hagsateriana,* 12) *Maxillaria ringens,* 13) *Maxillaria variabilis,* 14) *Mormodes lineata,* 15) *Mormolyca ringens,* 16) *Oeceoclades maculata,* 17) *Polystachya foliosa,* 18) *Stanhopea saccata,* 19) *Trigonidium ergotonianum.*

upon fracture, the majority of the pollen grains split open, as for the two species of Stanhopeinae (FIGURE 1:4, Nos. 5, 18). *K. tinschertiana* has a compact hard 1 texture (FIGURE 1:4, No. 6) with a rhomboid arrangement of the tetrads.

The ornamentation of the exine layer of the two species in Stanhopeinae (FIGURE 1:4, Nos. 5, 18) has small indentations or longer perforations on the external wall; *O. maculata* has laevigate to rugose ornamentation, and *K. tinschertiana* laevigate.

Comments upon the Methodology Used

Using low vacuum, intact, fresh pollinia were observed with their natural level of hydration, depending upon the original state of the flower. From these images it is possible to observe the size and arrangement of the pollinarium and the disposition of the caudicle in its natural state.

The processing of the pollinaria involves first a hydration of the pollinia to saturation, followed by a gradual dehydration using a series of graduated alcohols. In previous tests, 3% glutaraldehyde in a buffer solution of phosphates was used to fix the pollinia, but the results were the same as for the process without glutaraldehyde and it was, therefore, eliminated.

The techniques and processes used provoked various changes, such as an increase in the size of the pollinia, dissolution of the elastoviscin which in turn caused a loss of consistency of the pollinarium structure, and the deposition of partially dissolved residues on the surface of the pollinia. Elastoviscin does not resist treatment by acetolysis, differing from viscin which does resist this treatment (Schill & Wolter 1986). Elastoviscin may be lost during the processing of the pollinia if not first treated with osmium tetraoxide, whose molecules entwine with the lipid molecules, giving greater support (Fitzgerald et al. 1994). We did not use osmium tetraoxide and maybe lost part of the elastoviscin present in the samples. However, our methods permitted the observation of important characteristics which are essential for the characterization of the pollinia, such as the arrangement of the tetrads and the sculpture of the exine layer. The response to the treatment itself represents a further diagnostic aid.

With respect to the procedures used, the pollinia of the different orchid species studied showed different responses: some maintained the same size as that of the fresh state, as observed for *B. nodosa, M. trinasutum,* the two species of *Guarianthe* and the two *Pelexia* sp. The majority of the pollinia showed minimal swelling with an increase in size of less than 10%, as in the case of *C. integerrimum, G. galeata, L. labiatus, Isochilus* and *Epidendrum.* Others, such as those of *Encyclia* and *Prosthechea,* were variable: some retained the same size after processing, such as *P. ochracea,* whereas others swelled by up to 50%, such as *P. chondylobulbon.*

Observations under low vacuum were shown to be a very useful tool in this study, giving a clear image of the form, arrangement and size of the pollinia within an intact pollinarium. The fracture was carried out on pollinia dried to the critical point with CO_2, using fine pins, and is equivalent to the techniques recommended for the fracture of frozen samples in order to expose the internal surface, thus facilitating detailed observation of the arrangement of the tetrads and the level of compaction within the pollinium.

Because information concerning the SEM analysis of the morphology of pollinia is scarce, there are few comments concerning the effects of these procedures upon the pollinia. However, we show that observations using a combination of high and low vacuum generated sufficient information about the morphology of the pollinia of Soconuscan orchids to permit the identification of complete pollinaria or pieces of these, which is especially useful for pollination studies in which organisms are captured with a pollinium adhered to some part of the body.

In those species where it was possible to make a repeat analysis, the same or very similar results were obtained, suggesting that the procedures used were the correct ones and give reliable results, sufficient to enable the identification of orchid pollinia.

We differ with Balogh (1982) who found characteristics that united genera but not species; our results distinguish clearly between species but fall short of describing characteristics that unite species at genus level.

Pollination

The forms, colors and fragrances of orchid flowers, the rewards (or lack of reward) offered to pollinators, and the form and position of the pollinia and pollinarium, both within the flower and during transport by pollinators, are partially determined by the evolutionary history of the pollination process of each orchid species. However, that history is usually unknown, and the present-day form of a flower may have developed in response to previous and very different environmental conditions and pollinators. The responses of an orchid plant to the prevailing environmental conditions and to the range of potential pollinators available at any one time, as well as the strategies employed to attract them, are also constrained genetically. Indications are that it is the orchids that adapt to the pollinators, not vice versa; and that genetic drift also plays an important role in the great diversity of orchid pollination strategies (Tremblay et al. 2005, Gill 1989).

From our observations of the morphology of the pollinia, we can infer that those pollinia that are firmly united to the caudicles and easily separated (e.g., as in the case of *Encyclia),* could be transported separately by one or more pollinators. On the other hand, those that are hyaline and fused together must be transported together, by the same pollinator, in groups of two or four, depending upon the nature of the fusion. However, in the case of some *Epidendrum* species, the pollinia may be deposited in different flowers due to the fragility of the connection between the caudicle and pollinia (threads of viscin can be observed).

The pollinators of orchids are as diverse as the flowers in terms of size, form, behavior, and what they are looking for in a flower. Orchids exploit both the weaknesses and strengths of their pollinators to achieve fertilization and the persistence of their populations. The relationship between pollinia morphology and the pollinator has been little studied. We need to know more about the behavior of the pollinators and the efficiency of pollinia delivery. Does the pollinator visit only one or several species of flowering plants? Do the pollinia have to stay put while the messenger visits other types of flowers and fulfills other activities? Does the pollinator fly in the rain? Is the pollinator a fast flier, does it squeeze into fissures and tunnels, does it groom itself or get groomed by conspecifics? How long does it take for the pollinator to come into contact with another orchid flower of the same species? For how long do the pollen grains remain viable and what might affect that viability? These are questions that we hope to be able to answer in the future as our research continues.

Acknowledgements

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Literature Cited

Ackerman, J.D. and N.H. Williams. 1981. Pollen morphology of the Cloraeinae (Orchidaceae: Diurideae) and related subtribes. American Journal of Botany 68: 1392–1402.

Balogh, P. Pollinarium morphology of Mexican Orchi-

daceae (Laeliinae). Orquídea (Mex.) 8(2) 330–341.

Buchner, R. and M. Weber. 2000. PalDat—a palynological database: Descriptions, illustrations, identification, and information retrieval. In Web site: http://paldat.botanik.univie.ac.at/. Consultation carried out 8/12/2005.

Chase, M.W., K.M. Cameron, R.L. Barrett, and J.V. Freudenstein. 2003. DNA Data and Orchidaceae systematics: a new phylogenetic classification. *In* K.W. Dixon, S.P. Kell, R.L. Barrett, and P.J. Cribb, eds. Orchid Conservation. Kota Kinabalu, Natural History Publications (Borneo): 69–89.

Cribb, P.J. 1999. Morphology. *In* A.M. Pridgeon, P.J. Cribb, M.W. Chase, and F.N. Rasmussen, eds., Genera Orchidacearum, Vol. 1. General introduction, Apostasioideae, Cypripedioideae. Oxford University Press, Great Britain.

Dressler, R.L. 1981. The Orchids: Natural History and Classification. Harvard University Press, USA.

———. 1993. Phylogeny and classification of the orchid family. Cambridge University Press, Australia.

Faegri, K. and J. Iversen. 1989. Textbook of pollen analysis. The Blackburn Press, Norway.

Fitzgerald, M.A., S.H. Barnes, S. Blackmore, D.M. Calder, and R.B. Knox. 1994. Pollen development and cohesion in a mealy and hard type of orchid pollinium. International Journal of Plant Sciences 155: 481–491.

Freudenstein, J. and F.N. Rasmussen. 1996. Pollinium development and number in the Orchidaceae. American Journal of Botany 83: 813–824.

Gill, D.E. 1989. Fruiting failure, pollinator efficiency, and speciation in orchids. Pp. 458–481 *in* D. Otte and J. Endler, eds. Speciation and its consequences. Sinauer Associates, Sunderland, Mass.

Hesse, M., P. Burns-Balogh, and M. Wolff. 1989. Pollen morphology of the "primitive" epidendroid orchids. Grana 28:261–278.

Konta, F. and M. Tsuji. 1982. The types of pollen tetrads and their formation observed in some species in the Orchidaceae in Japan. Acta Phytotax. Geobot. 33: 206–217.

Moore, P.D., J.A. Webb, and M.E. Collinson. 1991. Pollen Analysis. Second Edition. Blackwell Scientific Publication. Oxford.

Pacini, E. and M. Hesse. 2002. Types of pollen dispersal units in orchids, and their consequences for germination and fertilization. Annals of Botany 89: 653–664.

Palynology glossary. In Web site: http://www.bio.uu.nl/~palaeo/glossary/glos-lit.htm. Consultation carried out 1/11/2003.

Roubik, D.W. 2003. Pollen and Sport of Barro Colorado Island. In Web site: http://striweb.si.edu/roubik/. Consultation carried out 09/26/2006.

SACDT. Systematics Association Committee for Descriptive Terminology. 1962. II. Terminology of simple symmetrical plane shapes. Taxon XI (5): 145–156, 245.

Schill, R. and M. Wolter. 1986. On the presence of elastoviscin in all subfamilies of the Orchidaceae and the homology to pollenkitt. Nord. J. Bot. 6: 321–324.

Schlee, D. and F. Ebel. 1983. Note on the chemical nature of the adhesive of viscid discs in *Catasetum finbriatum* Lindl. (Orchidaceae). American Journal of Botany 70: 872–876.

Singer, R.B. and S. Koehler. 2004. Pollinarium morphology and floral rewards in Brazilian Maxillariinae (Orchidaceae). Annals of Botany 93: 39–51.

Solano, R. and M. Soto Arenas. 2003a. *Stelis quadrifida* (La Llave & Lex.). Icon. Orchid. 5–6: xi.

———. 2003b. *Stelis greenwoodii* Soto Arenas & Solano. Icon. Orchid. 5–6: t. 682.

Stearn, W.T. 1966. Botanical Latin. Thomas Nelson and Sons Ltd. London.

Stenzel, H. 2000. Pollen morphology of the subtribe Pleurothallidinae Lindl. (Orchidaceae). Grana 39: 108–125.

Tremblay, R.L., J.D. Ackerman, J.K. Zimmerman, and R.C. Calvo. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. Biological Journal of the Linnaen Society 84: 1–54.

Yeung, E.C. 1987a. Development of pollen and accessory structures in orchids. Pp. 197–225 *in* J. Arditti, ed. Orchid biology reviews and perspectives, Vol. IV. Cornell University Press. USA.

———. 1987b. The development and structure of the viscidium in *Epidendrum ibaguense* H.B.K. (Orchidaceae). Botanical Gazette 148: 149–155.

Zavada, M. S. 1990. A contribution to the study of pollen wall ultrastructure of pollinia. Annals of the Missouri Botanical Garden 77: 785–801.